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The fecundity and histology of ovarian recrudescence in the yellow perch (*Perca flavescens* Mitchill) from selected lakes in Alberta

by

Carlito Habitan Mance

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Zoology

EDMONTON, ALBERTA

Spring 1987

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The fecundity and histology of ovarian recrudescence in the yellow perch (*Perca flavescens* Mitchill) from selected lakes in Alberta submitted by Carlito Habitan Mance in partial fulfilment of the requirements for the degree of Master of Science.

W.C.M. Mackay
Supervisor

D.E. Stevenson

D. Rimmer

Royal D. Ruth

Date 30 March 1987

Dedication

This piece of work is humbly dedicated to

my beloved parents

who taught us the value of education.

ABSTRACT

The purpose of this study was to examine aspects of fecundity and ovarian development in yellow perch from near the northern limits of their range. The time course of fecundity was monitored to determine when final fecundity is fixed in the fish. The best predictor of egg production was established by relating fecundity to body size and age. The variability of fecundity in populations showing different growths was also studied. The histological studies examined the time course of various cytological changes in the ovary and related these to changes in ovary weight (GSI).

Change in fecundity in a yellow perch population from a small Alberta lake was studied over a period of one annual ovarian cycle from May 1983 to March 1984. Additional perch were collected from 3 other lakes in February 1984 to determine the relationship between fecundity and growth rate. Fecundity was determined gravimetrically. Ovarian recrudescence was studied in females sampled from one of the lakes between May 1983 and March 1984. Ovaries were examined histologically using gluteraldehyde fixation and plastic embedding.

Fecundity declined significantly between October 1983 and March 1984 due to preovulatory degeneration of oocytes and to the possible inclusion in the fall oocyte counts of larger-sized resting oocytes. Perch from slow-growing populations were more fecund at a common length than their fast-growing counterparts from another lake, i.e., fecundity was inversely proportional to growth rates.

Histology showed that oocyte recruitment occurred at the end of the primary growth phase in late June. Recruitment was not accompanied by any increase in GSI and preceded peak feeding activity in the summer. Perch appear to recruit a large number of oocytes into recrudescence immediately after spawning and this number is modulated downward by as yet unidentified factors. When compared with a previous report on the histology of ovarian recrudescence in the Eurasian perch, that of the yellow perch differed in the 1) number of chorionic layers; 2) time of initiation of vitellogenesis in primary oocytes, 3) presence of preovulatory atresia, and 4) presence of both yolk vesicles and yolk granules that could be

easily distinguished by staining and location within the ooplasm.

The decline in the number of developing oocytes in the ovary of the fish in late winter when the fish are presumably food limited, the inverse relationship of fecundity to growth rate, and recruitment of primary oocytes early in summer are all part of an adaptive strategy in the yellow perch living in a latitude where the proximate factors are extreme.

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I would like to express my sincerest appreciation to Dr. William C. Mackay, whose guidance, support, and encouragement made possible not only the completion of this study but also my coming to study at the University of Alberta. Mary Baker, Tom Boag, Jack Gonzales, Jackie Newcomb, Karl Schwalme, Pat Valestin, and Heidi Zwickel are acknowledged for their assistance in various aspects of my research. Dr. John Sumpter was most helpful in assisting me identify the maturity stages of the yellow perch ovary. The Tuazon, Abada, and Pineda families were most generous in providing encouragement, assistance, and "second homes" throughout my stay in Canada. Sheau Jou Yang and David Ngo are appreciated for the accomodation they provided me during the completion of the manuscript. The prayers and practical help of the pastor, members, and adherents of the Filipino Christian Alliance Fellowship will never be forgotten. Finally, I would like to thank deeply my patient fiance, Judy Tan Ai Furn, for her tremendous contribution to the completion of my degree.

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I. GENERAL INTRODUCTION

Fecundity in fish is not a random process of dividing the gonadal materials into many or few eggs. Rather it is a strategy of investing energy in gonadal materials over time (Wootton 1979) such that the survival in any given type of environment of the maximum number of offspring produced over the lifetime of the parent is ensured (de Vlaming 1974). How the gonadal material is divided into many or few eggs depends on the interplay between adaptive physiological processes in the fish and environmental factors (Scott 1979). Thus, fecundity is a very effective mechanism for adjusting the reproductive rate of a fish population to a changing environment (Nikol'skii 1969).

A. FECUNDITY DEFINED

Absolute fecundity in fish is defined as the number of maturing eggs present in the ovary just before spawning (Bagenal 1978). It includes all mature ova about to be spawned and, in batch spawners, those maturing oocytes which will develop further before being deposited later in the same spawning season (Mann and Mills 1979).

During spawning, mature eggs are released in single or in several clutches over a variable time period depending on the species and the prevailing environmental factors. It is easy to determine fecundity in temperate fish species whose reproductive cycles are based on a strong annual periodicity. In habitats characterized by pronounced ranges of environmental conditions, reproductive cycles are predictably recurrent every year with a brief delineated period of spawning. When seasonality is less pronounced, reproductive cycles are less clearly defined with longer spawning times. In the yellow perch, *Perca flavescens*, the eggs develop and mature synchronously, and are released in a single batch in the spring (Thorpe 1977a). Spawning populations of yellow perch have been documented to release eggs over a period ranging from 3 (Tsai and Gibson 1971) to 16 days (Thorpe 1977a). Aside from the yellow perch, the roach, *Rutilus rutilis*, is another example of a single batch spawner (Mackay and Mann 1969). The majority of fish are multiple batch spawners, i.e., their ovaries contain asynchronously developing oocytes that mature and are released in several batches over the

same spawning season. Multiple batch spawners include the bleak, *Alburnus alburnus* (Mackay and Mann 1969), dace, *Leuciscus leuciscus* (Mann 1974), killifish, *Fundulus heteroclitus* (Wallace and Selman 1978, 1981), summer flounder, *Paralichthys dentatus* (Morse 1981), haddock, *Melanogrammus aeglefinus* (Robb 1982), three-spined sticklebacks, *Gasterosteus aculeatus, G. wheatli, Pungitius pungitius* (Craig and FitzGerald 1982), and sablefish, *Anoplopoma fimbria* (Mason et al. 1983).

It is difficult to define fecundity in tropical fish. The absence of marked seasonal fluctuations, particularly near the equator, which serve as cues in initiating and terminating ovarian recrudescence in temperate fish, allows some species to spawn continuously. Examination of the ovary of *Sarotherodon* species in a pond in Nigeria disclosed batches of oocytes in successive stages of development suggesting that as soon as a clutch was released, another ripened, thus allowing year-round egg production (Ita 1971, cited by Johnson 1974). Scott (1974) reported that the elephantfish, *Mormyra kannume*, sampled from their breeding ground in Lake Victoria, Uganda, were in a gravid stage throughout the year except during July and August.

Nonetheless, the majority of tropical species do show varying degrees of seasonality in reproductive cycles since within the tropics, factors such as temperature, photoperiod, and rainfall, become increasingly seasonal with increasing latitude above and below the equator. Cichlids from the Great Lakes of Africa behave much like temperate fish with gonad maturation from the fall until early spring, and spawning in the spring (Fryer and Iles 1972).

Even under relatively aseasonal conditions, biotic factors, e.g., competition for nesting sites, may impose seasonality (Lowe-McConnell 1979). In Lake Jiloa in Nicaragua, the seasonality of spawning in nine cichlid species in the lake is partially determined by the regime in the biomass-dominant *Cichlasoma citrinellum*, which outcompetes all but two of the smallest species for nesting sites and possibly for food (McKaye 1977). The other species are able to breed only in the drier season when *C. citrinellum* is food-limited because of the absence of its preferred food. In equatorial areas characterized by constant temperature and photoperiod, seasonal flooding of bodies of water makes available nutrients that limit

biological cycles. Wind-induced current changes in deep lakes and seas may also influence the upwelling of nutrients which can serve as a seasonal environmental cue and, hence, impose some form of seasonality on breeding (Lowe-McConnell 1979).

B. FACTORS INHERENT TO FISH THAT LIMIT FECUNDITY

Body length

A close relationship exists between fecundity and body size, i.e., fecundity increases with length and weight. The relationship between length and fecundity is defined by

$$F = aL^b \qquad (1)$$

where F is absolute fecundity, L is body length, and a and b are constants derived from the data (Bagenal 1978). A logarithmic transformation of the form

$$\log F = \log a + b \log L \qquad (2)$$

gives a linear relationship (Bagenal 1957, 1963). This transformation equalizes the variance throughout the range of size of fish and solves the problem that variations in fecundity of larger females tend to be greater than those of smaller females. Based on 124 observations in freshwater and marine fish, the exponent b in equation 2 ranged from about 1.0 to 7.0, but values clustered between 3.25 and 3.75 (Wootton 1979). Simpson (1951) argued that the commonly observed cubic relationship of fecundity to body length could be explained by a geometric constraint: the germinal epithelium was so folded that it filled the volume of the ovary. Fecundity could be related to a volume and hence the cube of the length. The value for b tends to be higher in long-lived species with good postspawning survival than in short-lived species with high mortality after spawning (Wootton 1979).

The slope relating fecundity to fork length ranges from 2.704 (Sheri and Power 1969, recalculated by Tsai and Gibson 1971) to 3.999 (Muncy 1962) in the yellow perch, and from 2.453 (Jellyman 1980) to 3.043 (Bregazzi and Kennedy 1982) in the Eurasian perch, *Perca fluviatilis*. It is not known whether these slopes are significantly different from each other because no one has attempted to do analysis of covariance using the original data. The

exponential relationship of fecundity to body length has been documented for a wide range of species including the herring, *Clupea pallasii* (Katz 1948), long rough dab, *Hippoglossoides platessoides* (Bagenal 1957), brook trout, *Salvelinus fontinalis* (Wydoski and Cooper 1966), dolly varden, *Salvelinus malma* (Blackett 1973), dace, *Leuciscus leuciscus* (Mann 1974), summer flounder, *Paralichthys dentatus* (Morse 1981), catfish, *Clarias lazera* (Clay and Clay 1981), and sablefish, *Anoplopoma fimbria* (Mason et al. 1983).

After reviewing the relationship between size and fecundity in various species, Woodhead (1979) proposed that after a certain length is attained, senescence-linked changes in the ovary may lead to a reduction in egg production. As a consequence, the number of eggs per unit body length may appear to decrease although the absolute number of eggs has remained unchanged (Bagenal 1978). This phenomenon has been observed in the Eurasian perch by a number of researchers (Stehlik 1969; Federova and Vetkasov 1975; Bregazzi and Kennedy 1982), but has not been reported in the yellow perch. Hickling (1940) observed that the weight of ovaries of herring, *Clupea harengus*, increased with age more rapidly than fecundity. The absence of any increase in the size of the eggs indicates that the permanent tissue surrounding the oocytes increased disproportionately in older females. Similar age-related degenerative changes that could lead to declining fecundity in otherwise growing females have been documented in the ovaries of guppies, *Poecilia reticulata* (Woodhead and Ellett 1967), and Siamese fighting fish, *Betta splendens* (Woodhead 1974).

Body weight

Since body weight is highly correlated with body length, fecundity should also be closely related to body weight. The relationship is expressed as

$$F = aW^b \qquad (3)$$

where F is fecundity, W is body weight, and a and b are constants calculated from the data (Bagenal 1978). This relationship is approximately linear where b is close to 1. If total body weight is used, a spurious relationship is usually obtained since the greater number of eggs in more fecund fish will weigh more than those in less fecund females (Bagenal 1978). This bias

can be minimized by using somatic weight instead, or by weighing the fish immediately after spawning (Wootton 1973a).

The relationship between fecundity and somatic weight in the yellow and Eurasian perch is linear (Tsai and Gibson 1971; Brazo et al. 1975; Treasurer 1981), but Sheri and Power (1969) reported a semilogarithmic relationship between the two parameters. This semilogarithmic relationship may due to an overestimation of fecundity because Sheri and Power (1969) counted oocytes early in oogenesis in the summer. A linear relationship between somatic weight and fecundity has also been reported in the long rough dab, *Hippoglossoides platessoides* (Bagenal 1957, Pitt 1964), herring, *Clupea harengus* (Baxter 1959), brook trout, *Salvelinus fontinalis* (Wydoski and Cooper 1966), dolly varden, *Salvelinus malma* (Blackett 1973), summer flounder, *Paralichthys dentatus* (Morse 1981), sticklebacks, *Gasterosteus aculeatus, G. wheatlandi, Pungitius pungitius*, and *Apeltes quadracus* (Craig and FitzGerald 1982), the clupeid *Pellonula afzeliusi* (Ikusemiju et al. 1983), and groupers, *Epinephelus* spp. (Bouain and Siau 1983).

Craig (1974) and Jellyman (1980) reported that the number of maturing eggs per unit somatic weight is inversely related to the length of Eurasian perch ranging from 12.3 to 42.2 cm fork length. However, the only report on somatic weight specific fecundity for the yellow perch found no such trend for the range of 12.3 to 27.8 cm fork length (Sheri and Power 1969).

Age

The effect of age on egg production must be isolated from those of length and weight by appropriate statistical methods because of the close relationship between age and size. When this is done, the effect of age may be insignificant, e.g., plaice, *Pleuronectes platessa* (Simpson 1951), long rough dab, *Hippoglossoides platessoides* (Bagenal 1957; Pitt 1964), redfish, *Sebastes marinus* (Raitt and Hall 1967), and whitefish, *Coregonus* spp. (Zawisza and Backiel 1970), or significant, e.g., haddock, *Melanogrammus aeglefinus* (Hodder 1963), roach, *Rutilus rutilus* (Mackay and Mann 1969), Greenland halibut, *Reinhardtius*

hippoglossoides (Lear 1970), capelin, *Mallotus villosus* (Winters 1971), sprat, *Sprattus sprattus* (de Silva 1973), northern mottled sculpin, *Cottus b. bairdi* (Ludwig and Lange 1975), and dace, *Leuciscus leuciscus* (Wilkinson and Jones 1977). In cases where there is no effect of age, length or weight were clearly correlated with fecundity.

Based on his work in the sprat, de Silva (1973) suggested that a curvilinear relationship between fecundity and age may be typical of fish with long lifespan while a linear relationship is common among short-lived species. Findings in the short-lived dace by Wilkinson and Jones (1977) showed a curvilinear relationship and, hence, did not support de Silva's theory.

The relationship between fecundity and age has been reported to be semilogarithmic in the yellow perch (Sherri and Power 1969; Brazo et al. 1975) and linear in the Eurasian perch (Treasurer 1981). In these studies, age was consistently the least reliable predictor of fecundity because variation in the number of eggs within an age group is considerable, and the fecundity of an individual fish may overlap into two or three age groups. The value of age as a predictive tool in predicting perch fecundity should be reevaluated because no work has been done to test the effect of age on egg production independent of body size. A model using age-length interaction is more accurate in predicting fecundity in the northern mottled sculpin, *Cottus b. bairdi*, than a model using age or length alone in the same species (Ludwig and Lange 1975). After analyzing published data on the plaice, Gerking (1959) concluded that individual variation in fecundity was so great that the real effect of age might be masked.

Egg size

Egg size constrains egg number since a given weight of ovary could be partitioned into many small or few large eggs. This trade-off between egg number and egg size is seen clearly in the herring, *Clupea harengus*, where summer-fall spawners are more fecund but have smaller eggs than the winter-spring spawners (Hempel and Blaxter 1967). Ware (1975) suggested that this variation in egg size in the herring has survival value. Large eggs lead to larger larvae which are better able to survive the harsh conditions of winter and spring than

their smaller counterparts. The smaller eggs, which hatch during the summer and fall, take advantage of their larger numbers by ensuring the survival to sexual maturity of the larvae at times when they are subjected to heavy predation. This inverse relationship between the size and number of eggs is not always true. In the goby, *Cottus gobio*, the egg diameter and egg number vary independently (Abel 1973, cited by Wootton 1979).

The size of the egg in the Eurasian perch is directly proportional to body length (Craig 1974; Bregazzi and Kennedy 1982). Thorpe (1977b) reported a diameter range of 1.0 to 2.1 mm but Treasurer (1981) reported the smallest diameter was 0.9 mm for the Eurasian perch. Mansueti (1964) recorded a similar range of 1.0 to 2.1 mm diameter for the yellow perch. Trade-off in egg size and fecundity has not been documented in either species of perch. Comparison of egg size in similarly sized individuals from different populations of identical or different latitudes within the geographic distribution of the perch is still open to investigation.

Best predictor of fecundity

The regression of fecundity on either total or fork length has been commonly used to investigate the fecundity of a single population, and to compare fecundities between populations. Length explains a larger fraction of the observed variation in fecundity than either weight or age in the yellow perch (Muncy 1962; Tsai and Gibson 1971; Brazo et al. 1975), roach, *Rutilus rutilus*, bleak, *Alburnus alburnus* (Mackay and Mann 1969), catfish, *Clarias lazera* (Clay and Clay 1981), and summer flounder, *Paralichthys dentatus* (Morse 1981). On the other hand, weight is better correlated with fecundity than length in dolly varden, *Salvelinus malma* (Blackett 1973), groupers, *Epinephelus* spp. (Bouian and Siau 1983), and the clupeid *Pellonula afzeliusi* (Ikusemiju et al. 1983). However, there are complications when comparing fecundity in terms of weight between samples collected at different times of the year. In many species, somatic weight changes rapidly with the approach of the spawning season (Le Cren 1951; Wootton 1973b; Iles 1974) so that regression of fecundity on weight in samples of fish captured at different times cannot be validly compared. Bagenal (1978) concluded that it is most practical to use length in predicting

fecundity. The most satisfactory method for comparing the fecundities of different populations is to compare the regression equation relating absolute fecundity to length or weight. Comparison of the fecundity on length relationship has been commonly used in the perch literature (Thorpe 1977b).

C. ENVIRONMENTAL DETERMINANTS OF FECUNDITY

Food

Wootton (1979) calculated the mean energy content of eggs and gravid ovaries from 50 species as 23.48 kJ/g dry weight with 95% confidence limits of 22.75 and 24.21. Given the energy cost of egg production, food becomes an important environmental factor affecting fecundity. Lowered fecundity is associated with low food quality due to low primary productivity of the water or insufficient quantity resulting from intraspecific competition because of high population density. This correlation has been documented in natural populations of the wild speckled trout, *Salvelinus fontinalis* (Vladykov 1956), haddock, *Melanogrammus aeglefinus* (Hodder 1965), brown trout, *Salmo trutta* (McFadden et al. 1965), landlocked salmon, *Salmo salar* (Leggett and Power 1969), roach, *Rutilus rutilus* (Mackay and Mann 1969), and the cyprinodont *Poeciliopsis occidens* (Constantz 1974).

The mechanisms by which insufficient food supply affect fecundity have been demonstrated in various studies. Experimentally food-restricted fish may 1) restrict the number of oocytes that develop, e.g., three-spined sticklebacks, *Gasterosteus aculeatus* (Wootton 1973a); 2) resorb mature eggs, e.g., rainbow trout, *Salmo gairdneri* (Scott 1962); 3) suppress the oocytes from developing at all, e.g., winter flounder, *Pseudopleuronectes americanus* (Tyler and Dunn 1976); and, under natural conditions, 4) delay the resorption of residual eggs left from the previous spawning. The lack of resorption interferes with the recruitment of a new batch of oocytes, e.g., yellow (Scott and Crossman 1973) and Eurasian perch (Koshelev 1963, cited by Hokanson 1977). Zawisza and Backiel (1970) believe that there is a critical threshold for food below which fecundity is significantly reduced.

The response of fecundity to food supply entails plasticity in that it may or may not affect the size and weight of eggs. For example, laboratory results have shown that food restriction which lowers fecundity may result in larger-sized mature ova as seen in the brown trout, *Salmo trutta* (Bagenal 1969), or in no change in size as observed in the three-spined stickleback, *Gasterosteus aculeatus* (Wootton 1973a). The response to favorable food resources is also variable because it may or may not involve increased egg number with a host of compensatory changes in egg size and weight. Martin (1970) reported that following a shift to fish prey by the lake trout, *Salvelinus namycush*, in an Ontario lake, the number, size, and weight of eggs increased significantly. In contrast, comparison of fecundity at a common length for coho salmon, *Oncorhynchus kisutch*, from a productive lake and an unproductive lake revealed slightly fewer but larger and heavier eggs in the population from the productive lake (Stauffer 1976). Brown trout, *Salmo trutta*, from fertile streams have heavier ovaries than similarly-sized females from infertile streams, but the former are not necessarily more fecund (McFadden et al. 1965). This suggests that the eggs are heavier in the population from the fertile stream .

The correlation between fecundity and food supply has never been investigated in either the yellow or Eurasian perch. Adaptive response of size and weight of eggs to food resources in the two species is unknown. The unusually high slope of fecundity on fork length regression for the yellow perch from the Patuxent (3.728) and Severn (3.999) Rivers, both in Maryland, may be associated with their rich estuarine environment (Muncy 1962; Tsai and Gibson 1971). Bregazzi and Kennedy (1982) compared the fecundity of the Eurasian perch between years in a lake rapidly undergoing eutropication and noted no change in fecundity. Similarly, Mann (1985) detected no change in the fecundity of lake whitefish, *Coregonus clupeaformis*, in a lake artificially fertilized over a period of four years.

Population density

Population density operates in conjunction with food supply. For example, lake-dwelling rainbow trout, *Salmo gairdneri*, from high-density populations have lower

fecundity than those from low-density populations, and this is presumably due to more intense competition for food among the former (Scott 1962). The work of Warren (1973) on the guppy, *Poecilia reticulata*, was directed toward separating the effect of density from the effect of food availability. When water from a tank containing a high density of female guppies was supplied to another tank containing fewer females, there was a marked reduction in the number of stage III oocytes. Females kept at high density also had fewer ovarian stages and produced fewer young. It appears that fish are capable of releasing water-born stress factors, produced as a result of crowding, that inhibit oocyte recruitment and development. Increased behavioral interaction was suspected to have been the cause of lowered fecundity in a high density population of the northern pike, *Esox lucius* (Kipling and Frost 1969). However, no factor has been isolated to support the view that crowding leads to the release of stress chemicals that could depress fecundity.

There has been no study of the net effect of population density on the fecundity of the yellow perch. In the Eurasian perch, Le Cren (1951) noted that following a population decline in Windermere Lake, there was an increase in fecundity as a consequence of improved growth rate. Surprisingly, data collected from Slapton Ley by Bregazzi and Kennedy (1982) before and after the decline of the Eurasian perch population there showed no increase in fecundity.

Temperature and light

Although it is known that temperature indirectly affects fecundity by acting on the rate of food consumption of the fish, the effect of temperature has been analyzed independently. Low temperature may affect fecundity by restricting the number of oocytes that enter vitellogenesis or by inducing follicular atresia. Field observations by Shrode and Gerking (1977) demonstrated in the desert pupfish, *Cyprinodon n. nevadensis*, that small departures from the species temperature tolerance limits resulted in decreases in the number, size, and hatchability of eggs. The study also demonstrated that the period spanning early oogenesis to just before spawning was more sensitive to temperature fluctuations than the

period from spawning to fertilization. When the mean water temperature was colder than normal, Hodder (1963) noted increased atresia of oocytes in the haddock, *Melanogrammus aeglefinus*. Similarly, colder than normal water temperature has been correlated with interrupted spawning and increased incidence of atresia in the northern pike, *Esox lucius* (June 1970). In contrast, colder water temperature results in higher fecundity in the pink salmon, *Oncorhynchus gorbuscha* (Rounsefell 1957). In his review of the evidence from various species, Wootton (1979) proposed that spawning activity and the number and hatchability of eggs peak at an optimum temperature, and as temperatures change in either direction, fecundity declines.

The effect of photoperiod on fecundity is unclear. Changes in photoperiod can modify the number of spawnings in three-spined stickleback, *Gasterosteus aculeatus* (Baggerman 1957), and in the catfish, *Heteropneustes fossilis* (Sundararaj and Vassal 1976). No study has been conducted on the effect of temperature and light regime on the fecundity of perch.

Other environmental factors

Other environmental factors that affect fecundity include lake morphometry (Brylinska et al. 1975, cited by Bagenal 1978), water level (June 1970), chronic oxygen depletion (Brungs 1971), and environmental contaminants (Macek 1968, Carlson 1972). Parasitic infestation may also depress fecundity by interfering with ovarian maturation. Sticklebacks, *Gasterosteus aculeatus*, infested with the tapeworm *Schistocephalus solidus* had significantly lower gonadosomatic index (GSI) than noninfested females (Meakins 1974).

D. FECUNDITY AND GEOGRAPHIC RANGE

The relationship between fecundity and geographic range has also been explored (Bagenal 1966), and many of the ideas on this topic are embodied in the concepts of *r* and *K* selection (MacArthur and Wilson 1967). *R* selection is the type of selection that occurs in unstable environments where population size is regulated largely by density-independent factors such as extreme temperature and short breeding season. *R*-selected populations

typically exhibit high fecundity, early maturity, tendency toward single spawning, and high reproductive effort. *K* selection describes selection in stable environments where mortality is caused more by density-dependent factors, e.g., crowding and competition for food. *K*-selected populations usually show low fecundity, late maturity, multiple broods, low reproductive effort, and sometimes parental care. The plaice, *Pleuronectes platessa* shows r-selected traits, i.e., higher fecundity, in areas where fishing pressure had been unusually heavy (Bagenal 1978). The Great Lakes in Africa have *K*-selected species that allocate a large amount of energy to non-egg-producing activities such as nest-building, brooding and care for young, and viviparity (Lowe-McConnell 1979). Although fish span the *r-K* continuum and show a high degree of versatility in their reproductive strategies, it is difficult to predict these strategies using the theories of *r* and *K* selection alone. Thus, one might expect populations from near the limits of the geographic range, where abiotic factors may be regulating population size, to show *r* selected strategies. No published research has looked at the relationship between latitude and fecundity. In fact no study has looked critically at the factors which regulate fecundity in perch.

This thesis is divided into two parts. Chapter 2 deals with 1) temporal change in the fecundity of a wild population of female yellow perch, and 2) comparison of the fecundities of four lake populations of yellow perch around Edmonton, Alberta, which show different growth rates. Chapter 3 describes the histological cycle of the ovary with emphasis on the identification of stage and timing of oocyte recruitment. The observation of preovulatory degeneration is also described as a possible mechanism to explain the apparent decline in fecundity towards the spawning time.

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II. A COMPARATIVE STUDY OF THE FECUNDITY OF YELLOW-PERCH (*Perca flavescens* Mitchill) FROM SELECTED ALBERTA LAKES

A. INTRODUCTION

Fecundity in fish is defined as the number of developing eggs in the ovary just prior to spawning (Bagenal 1978). Although the fecundity of the Eurasian perch, *Perca fluviatilis* L., is well studied (Stehlik 1969; Craig 1974; Federova and Vetkasov 1975; Mann 1978; Jellyman 1980; Treasurer 1981; Bregazzi and Kennedy 1982), that of the yellow perch, *Perca flavescens* Mitchill, has been described in only four papers (Muncy 1962; Sheri and Power 1969; Tsai and Gibson 1971; Brazo et al. 1975). These investigations used fish collected at different times before spawning (Appendix 1, Table 1.1) based on the assumption that fecundity does not change once the oocytes have been recruited. However, this assumption has not been tested. Sheri and Power (1969) reported higher fecundity at a common length for yellow perch, which were obtained in the summer, than those captured just before spawning from lakes of almost identical (Brazo et al. 1975) or lower latitudes (Muncy 1962; Tsai and Gibson 1971). This may indicate a progressive decline in potential fecundity as spawning time approaches, or true differences in egg production between populations, or an artifact due to differences in the methods the authors used to estimate the number of developing eggs.

There is no single previous study for the yellow or the Eurasian perch that compares the fecundities in two or more populations. There is also no study done to compare the fecundities at a common size or age of populations with different growth rates. Although Treasurer (1981) collected Eurasian perch from two adjacent kettle-hole lakes, he pooled the samples (n = 15) to obtain a common fecundity on length regression, even though the populations from the two lakes had different growth rates.

Absolute fecundity values range from 3,035 to 157,042 for the yellow perch (Brazo et al. 1975; Thorpe 1977a) and 950 to 210,000 for the Eurasian perch (Thorpe 1977a). Fish of the same size in a single population or in different populations show variability in fecundity (Thorpe 1977b). Thorpe (1977a) considered differences in productivity between habitats, food

abundance, spawning conditions, and extent of exposure to wind within the same habitat to be responsible for this variation. For any given lake, fecundity can be predicted by its regression on the fork or total length, somatic weight, and age. In the yellow perch, the relationship of fecundity to total or fork length, total or gutted weight, and age is logarithmic, linear, and semilogarithmic, respectively (Muncy 1962; Tsai and Gibson 1971; Brazo et al. 1975). Sheri and Power (1969) reported that the fecundity on fork length, on somatic weight, and on age relationships are semilogarithmic. Depending on the population, either length (Tsai and Gibson 1971) or weight (Sheri and Power 1969) can best explain the variation in fecundity. Age is consistently the least reliable predictor of fecundity because variation in fecundity within an age group is large and the fecundity of an individual may overlap into two or more age groups (Sheri and Power 1969; Brazo et al. 1975). The fecundity on length relationship in the Eurasian perch is similarly logarithmic (Craig 1974; Mann 1978; Jellyman 1980; Treasurer 1981; Bregazzi and Kennedy 1982). The relationships between fecundity and both weight and age are linear (Treasurer 1981).

Yellow perch have an annual reproductive cycle with gonadal growth in the fall and winter, concluding with spawning in the spring. Spawning occurs as early as February (Thorpe 1977b) and as late as June (Sheri and Power 1969; Newsome and Leduc 1975) depending on the latitude. A water temperature range of 5 ° to 14 ° C triggers spawning and the first females deposit eggs at progressively higher temperatures as latitude decreases (Thorpe 1977b). During spawning each breeding female, identified by her large size and gravid belly, is closely followed by several mature males which release their milt close to her vent as a single strand of eggs is extruded. The eggs are adhesive and are attached to plants and debris in shallow water (Harrington 1947; Hergenrader 1969). Unlike most fish, the yellow perch have only one ovary which lies on the midline of the body below the swim bladder and above the digestive tract (Parker1942). The ability of yellow perch to use relatively unspecialized substrate for spawning allows them to colonize in all still and slow-moving freshwater bodies within their geographical range (Collette et al. 1977).

This research addressed two aspects of fecundity. First, does fecundity change with the approach of the spawning season? If it does change, is the magnitude significant? If significant, when is actual fecundity established? The problem was tackled in the present study by determining the fecundity of perch from a single population between October 1983 and March 1984. The fecundities of the fish at various times throughout the winter were compared to the initial estimate made in October.

Second, how do the fecundities of different populations with different growth rates compare? This question was dealt with by comparing the fecundities of yellow perch collected from four lakes in February 1984.

B. MATERIALS AND METHODS

Study lakes and sampling regime

To determine the change in fecundity over time, yellow perch were collected from Mayatan Lake (53° 30' N, 114° W) from 15 May 1983 to 15 March 1984. Fish were caught with Windermere traps (Worthington 1950) and by angling during the open water season. During the winter sampling was done entirely by angling.

To compare the fecundities of females from different populations with different growth rates, further samples were collected from Lac Ste. Anne (53° 42' N, 114° 28' W), Thunder Lake (53° 8' N, 114° 46' W), and Narrow Lake (54° 37' N, 113° 39' W) in February 1984. Sampling was done entirely by angling. Preliminary data revealed that yellow perch from these lakes had different growth rates.

Sample treatment and analysis

Fish captured during the open water season were killed immediately and brought fresh to the Lac Ste. Anne Biological Station. Those caught by angling during the winter months were frozen until they could be processed at the Fish Laboratory of the Department of Zoology at the University of Alberta. Total body length was measured to the nearest mm with

a measuring board. After blotting the body and gonad dry with paper towels, the somatic weight (total body weight minus gonad weight and weight of stomach contents) and gonad weight were measured to the nearest 0.01 g using an electronic balance.

The left opercular bone was removed for age determination following the method of Le Cren (1947).

Determination of fecundity

After weighing the ovary, the connective tissue envelope was slit open to expose the developing or maturing oocytes. Then the ovary was placed in fresh Gilson's fluid as modified by Simpson (1951). The fixed ovary was shaken every few weeks to facilitate dissociation. The ovary was kept in the fixative for a period of 8 to 10 weeks which was long enough to completely dissociate the oocytes from the connective tissue. The small-sized resting oocytes and debris were separated from the developing oocytes by repeated washing and decantation using tap water.

The washed oocytes were then layered on a filter paper, 12.5 cm across, placed in a Buchner funnel which had been fitted to a vacuum flask. A mild vacuum was used to remove excess water. The oocytes were then air-dried for at least 24 hours. No significant changes in weight of the samples were detected after 24 hours of drying.

The gravimetric method was chosen to determine fecundity in the present study. This method was selected over the volumetric method (Lagler 1956) because the latter tended to underestimate significantly the number of oocytes in the Eurasian perch (Treasurer 1981). Oocytes, including those from the Eurasian perch, have been observed to sink rapidly in water so that uniform and representative subsamples cannot be obtained with the volumetric method (Bagenal and Braun 1968; Craig 1974).

The total weight of developing oocytes from a single ovary was determined to the nearest 0.0001 g with the use of a Sartorius 2400 digital analytical balance accurate to 0.00001 g. Then three subsamples, each consisting of exactly 200 oocytes, were drawn from the oocytes of a single ovary, and each subsample was weighed. Fecundity was estimated by

multiplying by 200 the ratio of the total weight of the oocytes from that ovary to the average weight of the three subsamples.

Reliability of fecundity determination

To determine the reliability of the procedure for determining fecundity, ten triplicate weighings of subsamples of exactly 200 oocytes were taken with replacement from the total oocyte collection from one fish (Appendix 1, Table 2). The 200 oocytes were taken at random and were returned to the sample after each weighing. The mean of triplicate weighings was used to estimate the fecundity of the fish. Individual fecundity estimates differed by -1.39% to +2.24% from the overall mean estimate of 9,511 with a 95% confidence interval of 70. On average, each individual fecundity estimate varied by 0.93% from the overall mean fecundity estimate. This demonstrates the reproducibility of the estimation method. Hence, the variability in fecundity between individual fish was not due to significant error of the method used.

Comparison of fecundity within and between lakes

Fecundity on total length relationships were used, in preference to fecundity on somatic weight or age relationships, when comparing fecundity within a lake at different times of the year, or between lakes at the same time of the year. Comparison on the basis of fecundity on total length regressions has been commonly used in the perch literature (Thorpe 1977b; Tsai and Gibson 1971). Since somatic weight changes significantly with the approach of spawning (Le Cren 1951; Wootton 1973), use of the fecundity on somatic weight relationship is not reliable when comparing the fecundity of samples collected at various times. Age has been consistently found to be poorly correlated with fecundity compared to either length or weight in the yellow perch (Sheri and Power 1969; Tsai and Gibson; Brazo et al. 1975).

Growth rates of female yellow perch

In order to determine the growth rates of female yellow perch, the mean total lengths at different ages of 56 females from Mayatan Lake, 51 from Lac Ste. Anne, 47 from Thunder Lake, and 47 from Narrow Lake were backcalculated according to Le Cren's (1974) method.

C. RESULTS

Temporal changes in fecundity of yellow perch during gonad recrudescence

Yellow perch were collected from Mayatan Lake between 15 May 1983 and 15 March 1984, but only those females collected from 8 October 1983 onward were used in the estimation of fecundity. Developing oocytes in ovaries of females collected before October could not be macroscopically distinguished on the basis of size from the resting oocytes. Table 2.1 shows that from 8 October 1983 to 15 March 1984, a total of 148 females, ranging in size from 14.2 cm (lowest fecundity, 1,909) to 25.1 cm (highest fecundity, 19,333) were included in this part of the investigation.

For each monthly sample, the relationship between total length and fecundity was found to be exponential (Fig. 2.1; Appendix 1, Table 3; Appendix 2, Figs. 1 - 5). Logarithmic transformation of the data and regression of log fecundity on log length using the least square method provided the best fit of a straight line. The F statistics for the correlation coefficients between total length and fecundity were all highly significant (F value range 34.93 - 153.08, all $P < 0.001$). Simultaneous comparisons of the five regression lines, each representing a monthly sample, using analysis of covariance showed no significant differences between the slopes (Appendix 1, Table 4). When compared with the elevation of the October regression line, considered as the initial fecundity, the January, February, and March regressions declined significantly in elevation. Comparison between January, February, and March regression lines showed no significant differences in elevations. One-way analysis of variance for unequal sample sizes (Appendix 1, Table 5) showed no significant differences between the mean total lengths of similarly aged females collected between 8 October 1983 and 15 March

Table 2.1. Date of sampling, size of sample, range in total length and fecundity, and measures of central tendency of total length and fecundity of yellow perch from Mayatan Lake, Alberta.

Sampling Date	Sample Size	Range		Mean ± 95% C.L.[1]		Median ± 95% C.L.[1]	
		Total Length (cm)	Fecundity	Total Length (cm)	Fecundity	Total Length (cm)	Fecundity
1983							
8 October	34	15.2-25.1	2,921-19,333	19.2 ± 0.8	8,722 ± 1,386	18.9 ± 1.0	9,085 ± 1,987
5 December	24	15.5-21.0	2,102-12,360	17.2 ± 0.6	5,369 ± 916	17.0 ± 0.9	4,733 ± 662
1984							
14, 28 January	34	14.2-23.5	1,909-13,233	18.6 ± 1.2	6,395 ± 1,044	18.3 ± 0.8	6,099 ± 1,379
27 February	32	15.0-21.0	2,411-8,172	17.7 ± 0.5	4,962 ± 585	17.6 ± 0.6	4,646 ± 883
15 March	23	14.3-21.3	2,155-9,623	17.8 ± 0.7	5,202 ± 995	18.0 ± 0.5	4,454 ± 1,587

[1] C.L. - confidence limits

Fig. 2.1. Relationship between total length and fecundity for yellow perch collected from Mayatan Lake, Alberta, between 8 October 1983 and 15 March 1984. For clarity, only the data points for the sample collected on 8 October are shown. The lengths of the curves for the other dates correspond to the range of data. The 95% confidence limits of the regression estimates are shown in Appendix 2, Figs. 1 - 6.

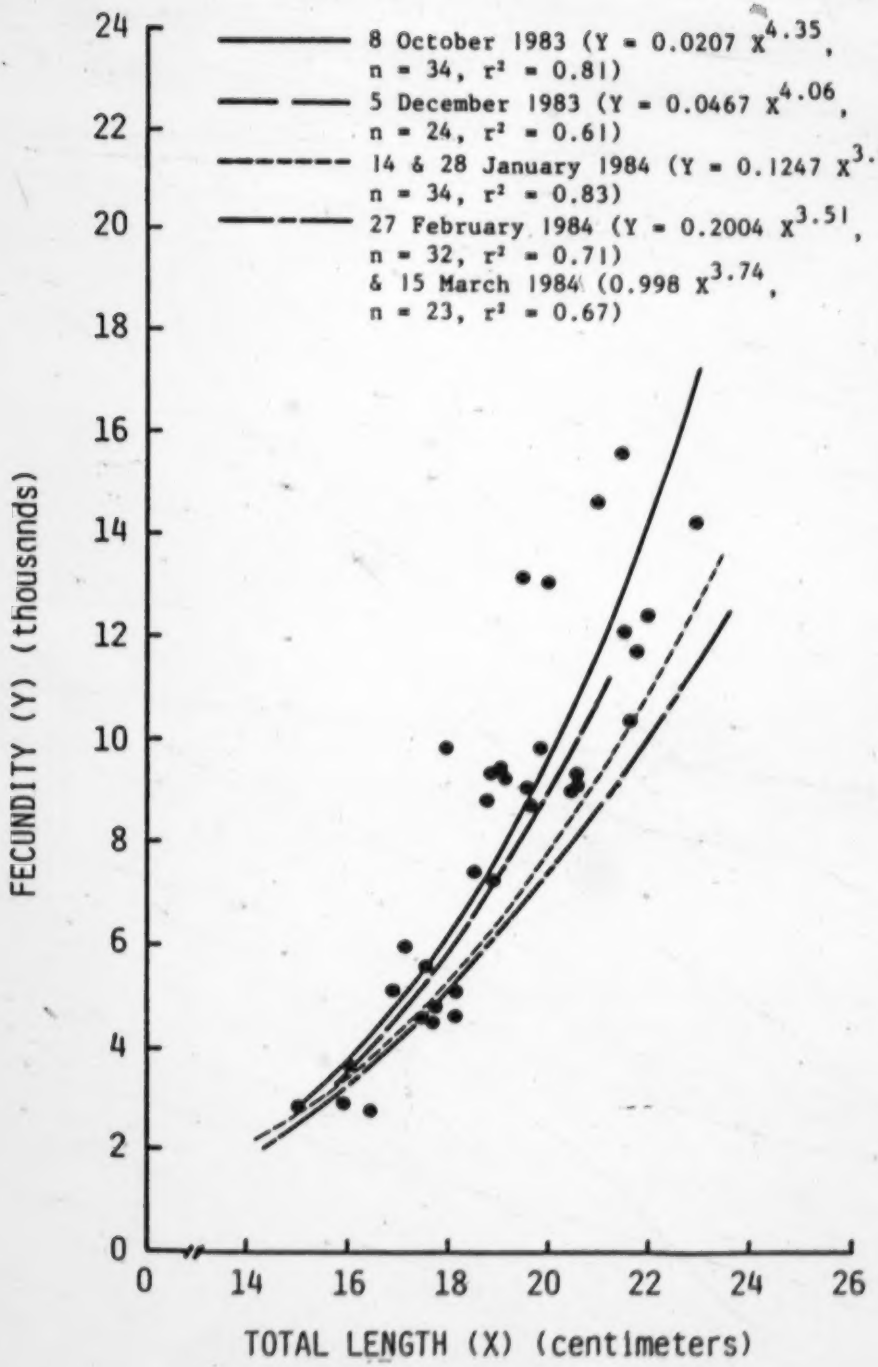


Fig. 2.1. Legend is on the opposite page.

1984. This does not support the possibility that the regressions of fecundity on total length declined in elevation because of an increment in the size of the fish over the sampling period. The fecundity of a female with a total length of 19.0 cm declined by 20% from October to March of the following year (Table 2.2).

Comparison of fecundities of yellow perch from four lakes

A total of 201 female perch, ranging in total length from 9.9 to 22.6 cm, were included in this part of the study (Table 2.3). The relationship between fecundity and total length in each lake was best described by a logarithmic equation (Fig. 2.2; Appendix 1, Table 6; Appendix 2, Figs. 6 - 9). Total length accounted for 75.3% (Mayatan and Thunder Lakes) to 96.03 (Narrow Lake) of the observed variation in fecundity. The fecundity on length regressions from the four lakes were then compared in terms of slopes and elevations using analysis of covariance.

The regression coefficient b for the relationship of log fecundity to log total length ranged from 3.360 (Lac Ste. Anne) to 3.822 (Thunder Lake). A test for significance of difference among correlation coefficients showed highly significant differences between all the lakes (F value range 74.60 - 382.29, all $P < 0.001$). Hence, there were very strong correlations between fecundity and total length in all four lakes.

Comparisons of the four relationships between fecundity and total lengths done using analysis of covariance revealed no significant differences between slopes ($P < 0.05$). However, the elevations were significantly different between lakes (Appendix 1, Table 7). Hence, the rates of change in fecundity with body length were the same for all the lakes, but the levels about which the change occurred were different. Egg production for a female adjusted to a total length of 16.5 cm was: Narrow Lake, 10,491; Lac Ste. Anne, 6,898; Thunder Lake, 5,662; and Mayatan Lake, 3,710.

Table 2.2. Fecundity of yellow perch calculated for three different total lengths on the dates of sampling. The fish were sampled from Mayatan Lake, Alberta, between 8 October 1983 and 15 March 1984.

	Total Length					
	15 - cm		19 - cm		23 - cm	
Sampling Date	Fecundity	% Decline[1]	Fecundity	% Decline[1]	Fecundity	% Decline[1]
8 October 1983	2,835	-	7,587	-	16,812	-
5 December 1983	2,805	1.06	7,330	3.39	15,932	5.23
14, 28 January 1984	2,658	6.25	6,345	16.37	12,815	23.77
27 February 1984	2,685	5.29	6,155	18.87	12,034	28.42
15 March 1984	2,519	11.15	6,101	19.59	12,474	25.80

[1]Percent decline in fecundity were calculated by considering the estimate made in 8 October 1983 as the initial fecundity.

Table 2.3. Size of sample, range in total length and fecundity, and measures of central tendency of total length and fecundity of yellow perch collected from four Alberta lakes.

Lake	Number of Females	Range		Mean ± 95% C.L.[1]		Median ± 95% C.L.[1]	
		Total Length (cm)	Fecundity	Total Length (cm)	Fecundity	Total Length (cm)	Fecundity
Mayatan[2]	89	14.2-23.5	1,909-13,233	18.1 ± 0.4	5,572 ± 518	18.0 ± 0.3	4,839 ± 816
Ste. Anne[3]	90	12.5-22.6	2,421-19,000	16.6 ± 0.4	7,536 ± 666	16.5 ± 0.8	6,832 ± 1,132
Thunder[4]	30	16.5-22.0	4,997-18,292	18.9 ± 0.5	9,780 ± 1,100	19.0 ± 0.6	9,751 ± 1,541
Narrow[5]	9	9.9-16.5	2,276-10,124	13.6 ± 1.8	5,395 ± 2,356	13.9 ± 3.4	5,560 ± 4,432

[1] C.L. - confidence limits

[2] Samples were collected between 14 January and 15 March 1984. The samples were pooled because of equality of slopes and elevations of log_{10} *fecundity* on log_{10} *total length* regressions at $P < 0.05$.

[3] Samples were collected on 23 February 1983 and 17 February 1984. The samples were pooled because of equality of slopes and elevations of log_{10} *fecundity* on log_{10} *total length* regressions at $P < 0.05$.

[4] Sample was collected on 22 February 1984.

[5] Sample was collected on 23 February 1984.

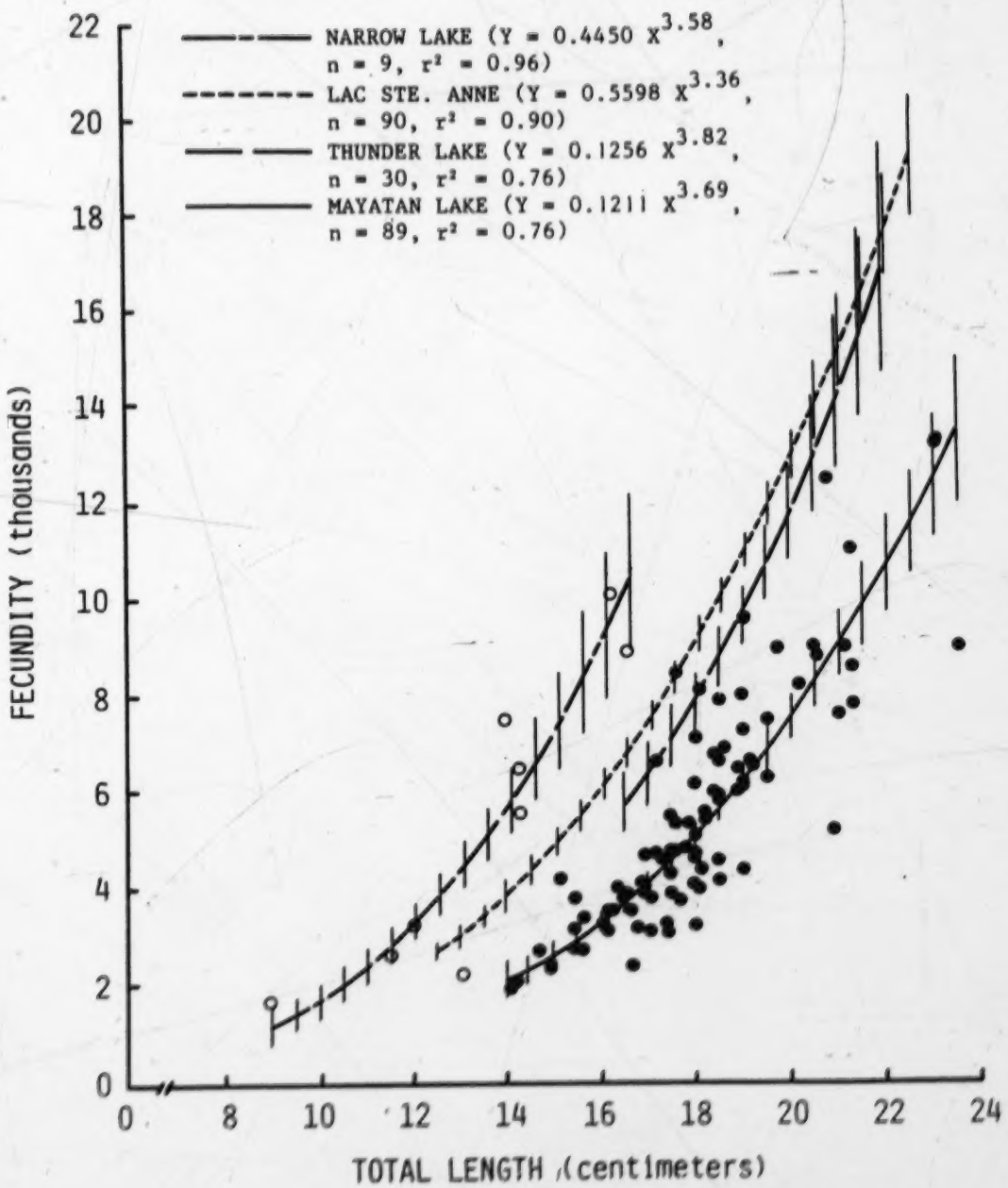


Fig. 2.2. Relationship between total length and fecundity for yellow perch collected from four Alberta lakes in February 1984. For clarity, only the data points from Narrow Lake (open circles) and Mayatan Lake (solid circles) are shown. The shaded areas correspond to the 95% confidence limits of the regression estimates.

Growth rates of females from four lakes

The growth curves for female perch from the four lakes are plotted in Fig. 2.3. Multiple comparisons of mean back-calculated total lengths of females of same age from different lakes were done using the Newman-Keul's test for unequal sample sizes (Table 2.4). Females from Thunder Lake were consistently the fastest growing but at ages V+ and VI+, their mean total lengths were not significantly larger than those of Mayatan Lake females ($P > 0.05$). The small sample size for Thunder Lake ($n = 3$) could explain the absence of any significant difference at age VI+ between the Thunder and Mayatan Lake females. The test might not be sensitive enough when the sample size is small. The females from Narrow Lake were always significantly smaller than those from the other three lakes.

Fecundity and growth rate

The data show that slow-growing populations from Narrow Lake and Lac Ste. Anne had higher fecundities at a common length than their fast-growing counterparts from the other two lakes (Fig. 2.2)

Length-specific relative fecundity

Figure 2.4 shows that the mean number of eggs per cm total length increased exponentially with the total length of the fish (Appendix 2, Figs. 10 - 13). The correlation coefficients between the two log-transformed variables for Mayatan Lake (0.75), Lac Ste. Anne (0.90), Thunder Lake (0.80), and Narrow Lake (0.96) were all highly significant (all F values $P < 0.001$). Females from Narrow Lake had the highest length-specific fecundity while females from Mayatan Lake had the lowest at any common length. The slopes of the length-specific fecundity on total length relationships could not be compared because of heterogenous variances.

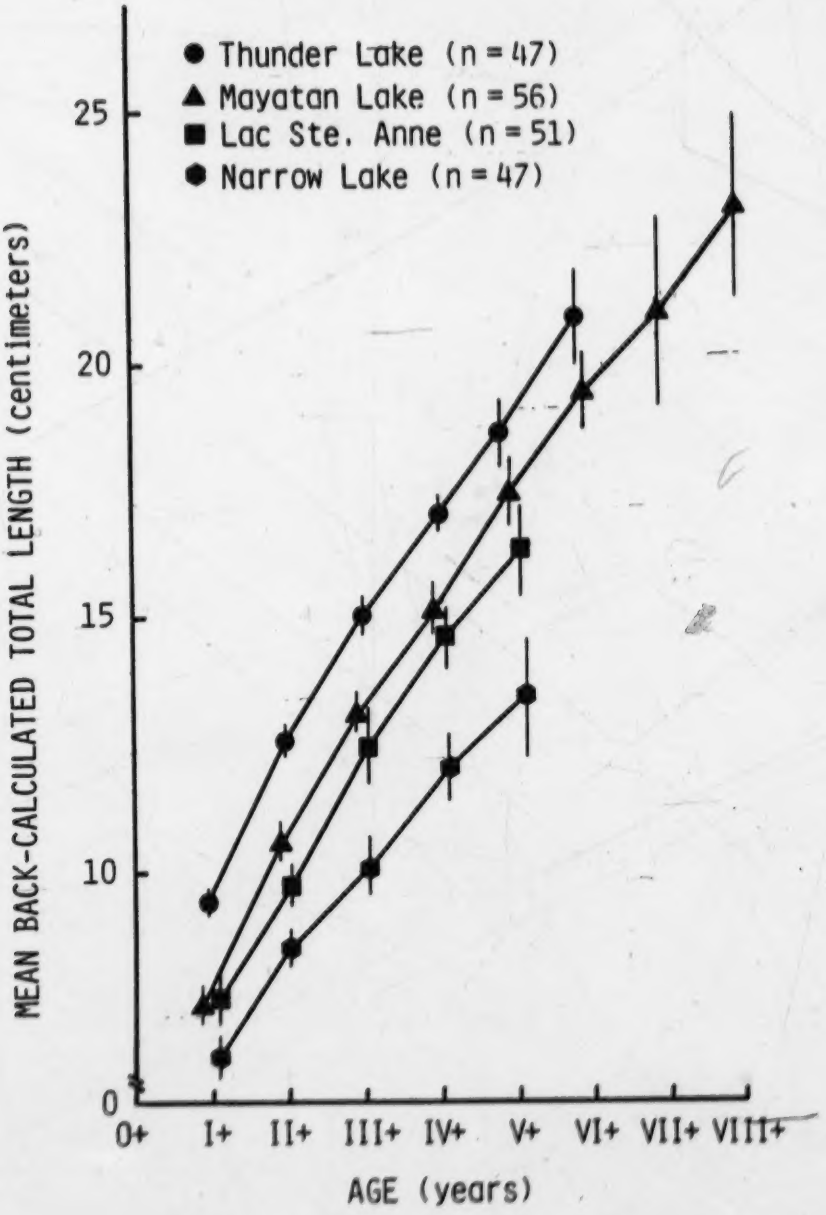


Fig. 2.3. Relationship between age and mean back-calculated total length for female yellow perch collected from four Alberta lakes. The bars above and below the data points represent the 95% confidence limits of the mean back-calculated total lengths.

Table 2.4. Multiple comparison of mean back-calculated total lengths at different ages of female yellow perch collected from four Alberta lakes.[1]

Age Group	Mean Back-Calculated Total Length (cm)[2]			
	Mayatan Lake	Lac. Ste. Anne	Thunder Lake	Narrow Lake
I+	7.42[a]	7.53[a]	9.44[b]	6.36[c]
	(56)	(51)	(47)	(47)
II+	10.56[a]	9.68[b]	12.57[c]	8.47[d]
	(56)	(51)	(47)	(45)
III+	13.13[a]	12.35[b]	15.02[c]	10.14[d]
	(55)	(41)	(47)	(40)
IV+	15.13[a]	14.60[a]	17.00[b]	12.01[c]
	(49)	(29)	(40)	(26)
V+	17.41[ab]	16.34[a]	18.62[b]	13.37[c]
	(35)	(22)	(15)	(14)
VI+	19.40[a]	17.19[b]	20.89[a]	-
	(21)	(7)	(3)	-
VII+	21.02[a]	21.45[a]	-	-
	(6)	(4)	-	-

[1] Mean back-calculated total lengths for each age were compared using the Studentized Newman-Keul's method at the significance level of 0.05. Ho: there was no significant difference in the total lengths of female fish of the same age from various lakes.

[2] Mean back-calculated lengths at any one age with a common superscript were not significantly different at $P < 0.05$. Numbers in parentheses correspond to sample size.

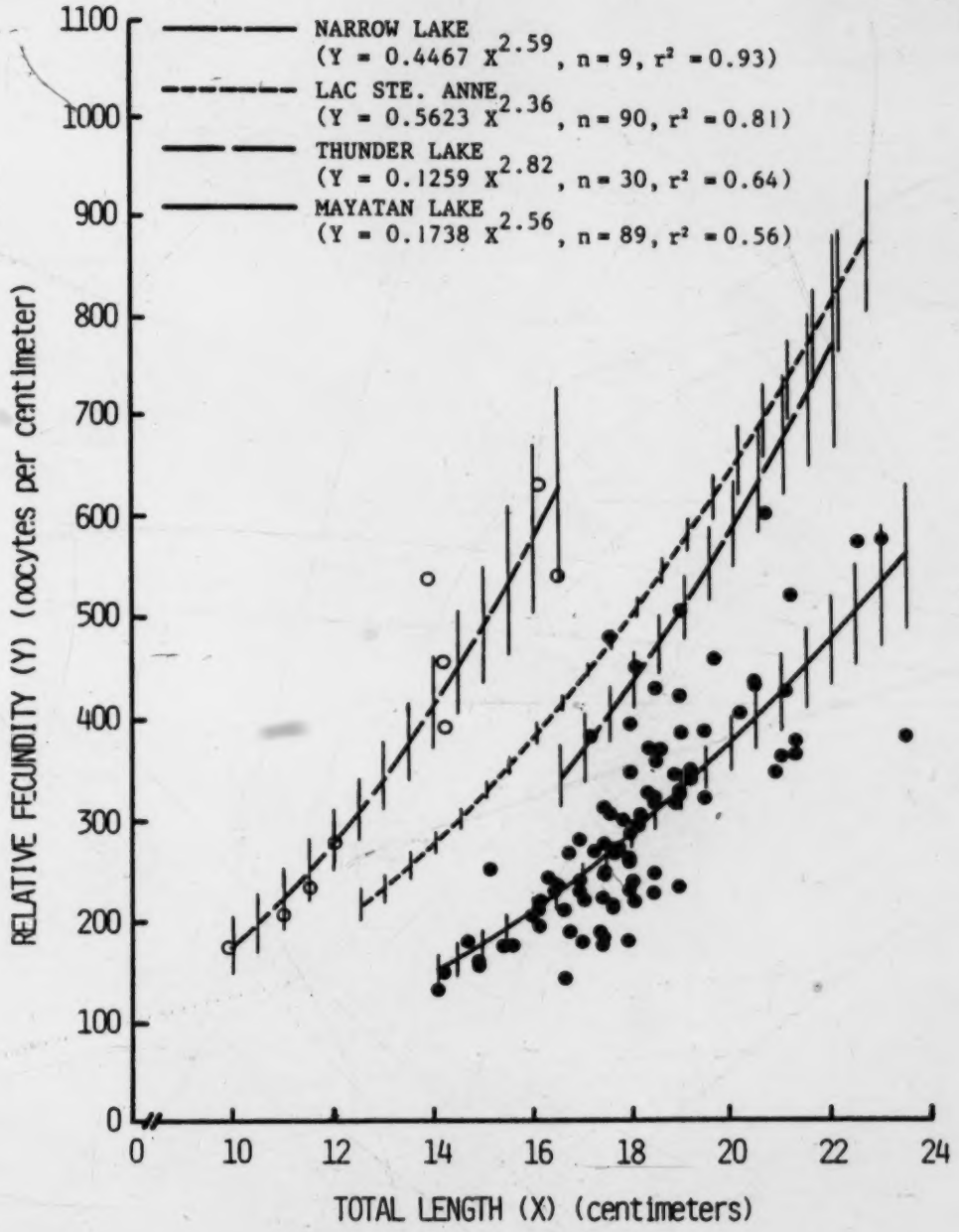


Fig. 2.4. Relationship between total length and length-specific fecundity for yellow perch collected from four Alberta lakes in February 1984. For clarity, only the data points from Narrow Lake (open circles) and Mayatan Lake (solid circles) are shown. The shaded areas correspond to the 95% confidence limits of the regression estimates.

Somatic weight and fecundity

The relationships between somatic weight and fecundity in all the lakes were linear. The correlation coefficients for these relationships were all highly significant (F value range 100.97 - 507.64, all P <0.001). Somatic weight was able to explain a larger portion of the observed variation in fecundity than total length (Appendix 1, Table 8 - 12). The fecundity on somatic weight regressions are plotted in Figure 2.5 (Appendix 2, Figs. 14 -17). Mean egg production for a 42.0-g female was 11,858 for Narrow Lake, 6,559 for Lac Ste. Anne, 5,579 for Thunder Lake, and 4,548 for for Mayatan Lake. This represents a 2.6 fold difference in fecundity between the most and the least fecund populations at a single body weight.

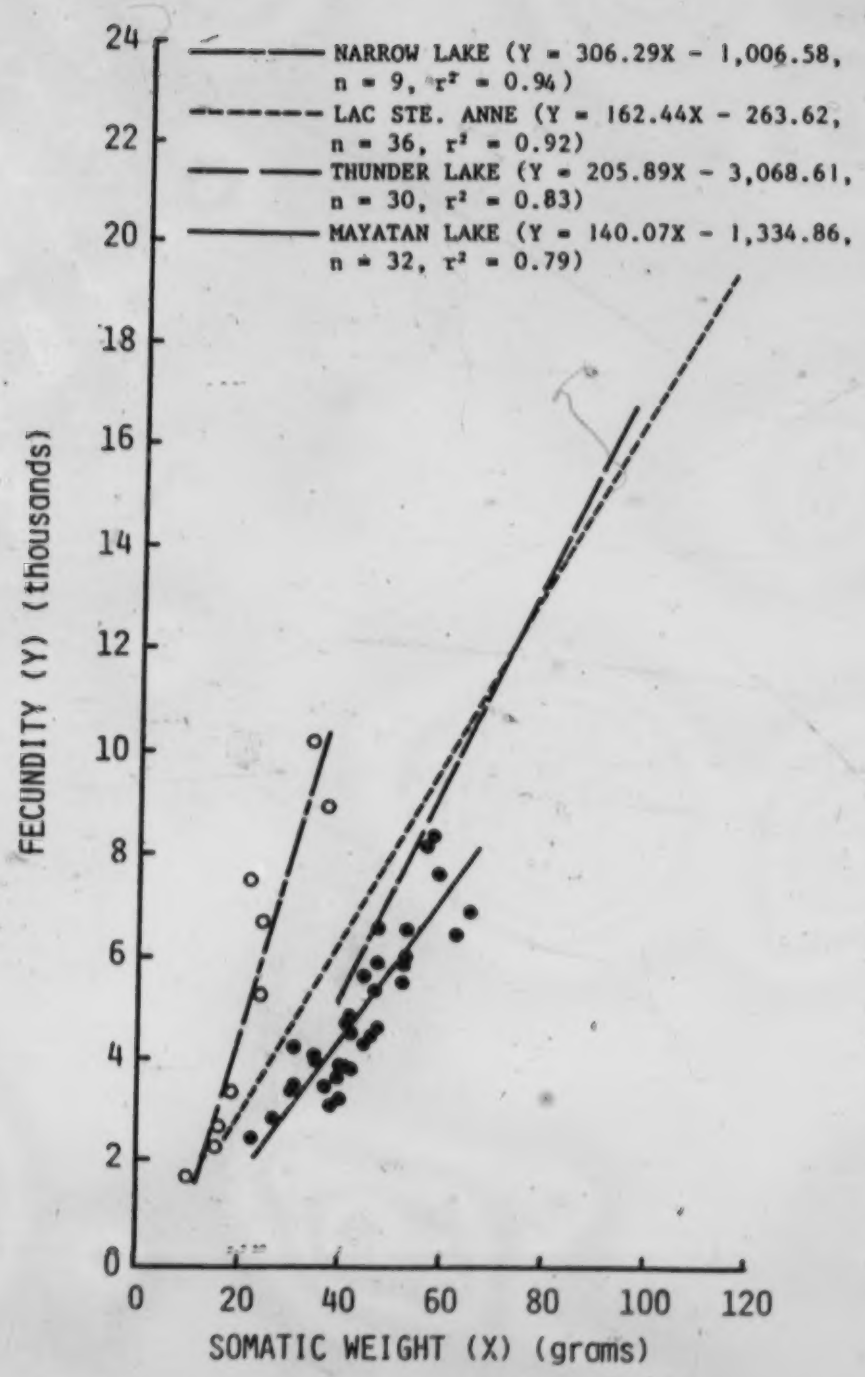
Weight-specific relative fecundity

The numbers of oocytes per gram of somatic weight were not significantly correlated with somatic weight for fish taken from Mayatan Lake ($r = 0.22$; F value $P > 0.05$), Lac Ste. Anne ($r = 0.03$; F value $P > 0.05$), and Narrow Lake ($r = 0.63$; F value $P > 0.05$) (Appendix 2, Figs. 18, 19, 21). The relationship between the two variables was significant for Thunder Lake ($r = 0.46$; F value $P < 0.01$) where the relative fecundity increased linearly with the somatic weight (Appendix 2, Fig. 20). The coefficients of variation for fecundity (0.30) and somatic weight (0.21) for Thunder Lake were the lowest among the four lakes. This could account for the fact that only in Thunder Lake was there a significant correlation between the number of oocytes per gm and somatic weight.

Ovary weight and fecundity

There was a linear relationship between ovarian weight and fecundity for fish from the four lakes studied (Appendix 1, Table 9). F-statistics for the correlation coefficients were all consistently high in significance (F value range 86.97 - 2,579.56, all P <0.001). The scatter diagrams are shown in Figure 2.6 (Appendix 2, Figs. 22 - 25). Ovary weight explained 74% (Mayatan Lake) to 98% (Narrow Lake) of the observed variability in fecundity. This indicates that in some lakes, there were marked differences in oocyte size and/or amount of

Fig. 2.5. Relationship between somatic weight and fecundity for yellow perch collected from four Alberta lakes in February 1984. For clarity, only the data points from Narrow Lake (open circles) and Mayatan Lake (solid circles) are shown. The lengths of the lines correspond to the range of data. The 95% confidence limits of the regression estimates are shown in Appendix 2, Figs. 14 - 17.



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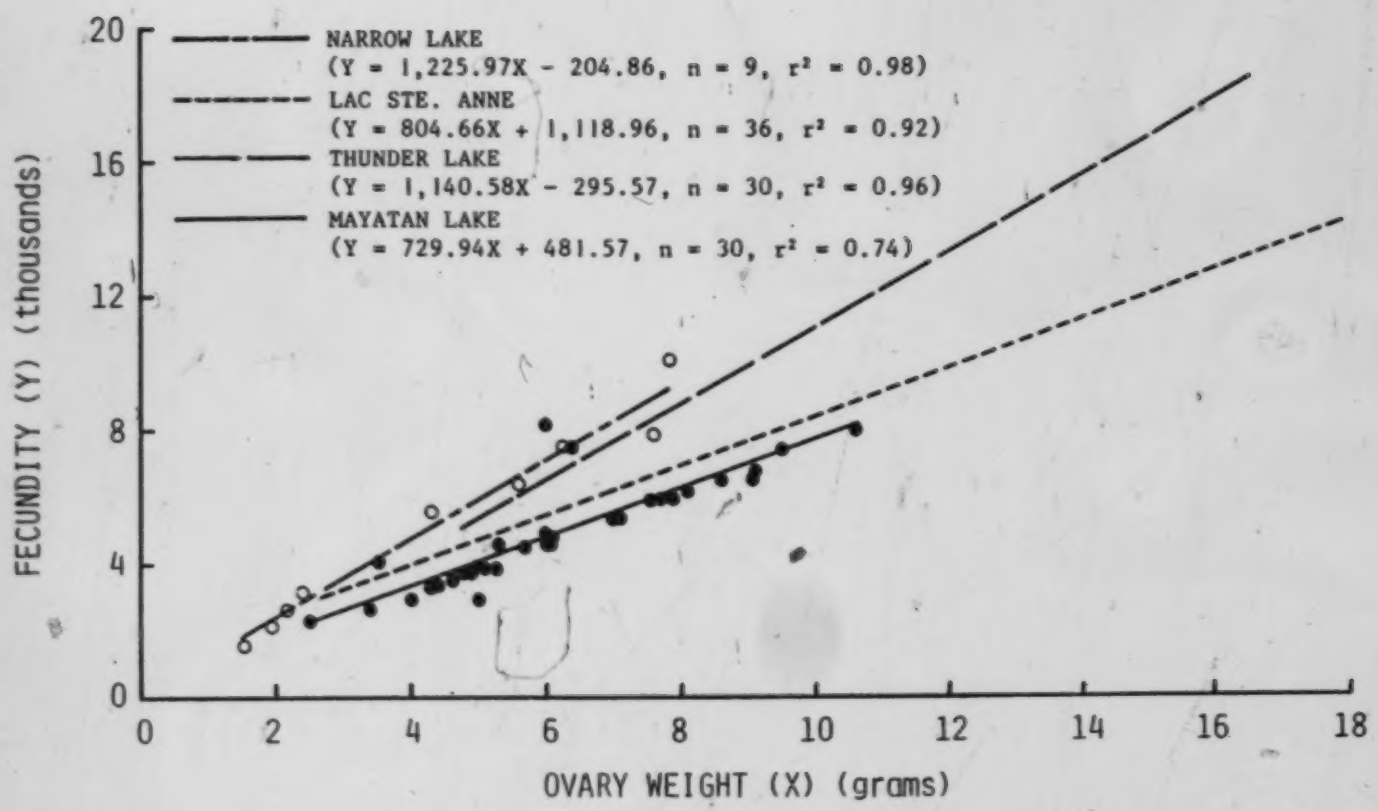

Fig. 2.6. Relationship between ovary weight and fecundity for yellow perch collected from four Alberta lakes in February 1984. For clarity, only the data from Narrow Lake (open circles) and Mayatan Lake (solid circles) are shown. The lengths of the lines correspond to the range of data. The 95% confidence limits of the regression estimates are shown in Appendix 2, Figs. 22 - 25.

connective tissue at a given ovary weight.

Age and fecundity

A logarithmic regression best described the relationship between fecundity and age in three of the lakes (Fig. 2.7; Appendix 1, Table 10; Appendix 2, Figs. 26 - 29). However, the correlation coefficients were low compared to those of fecundity on total length or somatic weight or ovary weight relationships. This could mean that factors other than age contribute substantially to the variation in fecundity. The fecundity on age relationship for Thunder Lake was linear (Fecundity = 2352.73 Age - 22.70; r = 0.52; F = 10.20, P <0.005). Hence, the rate of increase in fecundity with age was far slower for Thunder Lake (b = 0.80) than Mayatan Lake (1.43), Lac Ste. Anne (1.61), and Narrow Lake (1.68). The variations in absolute fecundities were considerable to the extent that the range in each age group sometimes overlapped into two or three other age groups. Age was able to account for from a low 27.04% (Thunder Lake) to 86.49% (Narrow Lake) of the observed variation in fecundity. Hence, age was the least reliable predictor of egg production.

At all ages, the females from Thunder Lake showed the highest fecundity while those from Mayatan Lake showed the lowest (Fig. 2.7). Females from Mayatan Lake matured later than those from the other lakes. Table 2.5 compares the mean fecundities of the various age groups from all four lakes (Appendix 1, Table 11).

Best predictor of fecundity

The four independent variables, total length, somatic weight, ovary weight, and age, were all highly correlated both with fecundity and with each other (Appendix 1, Table 12). Hence, it was highly probable that an apparent correlation of the dependent variable (fecundity) with one of the four presumably independent variables could have been spurious and due primarily to its correlation with a second independent variable. In order to determine net relationship between each of the independent variables and fecundity, without interactions among the independent variables, a series of logarithmic multivariate regression analyses of

Fig. 2.7. Relationship between age and fecundity for yellow perch collected from four Alberta lakes in February 1984. For clarity, only the data points from Thunder Lake (open circles) and Mayatan Lake (solid circles) are shown. The lengths of the lines correspond to the range of data. The 95% confidence limits are shown in Appendix 2, Figs. 26 - 29.

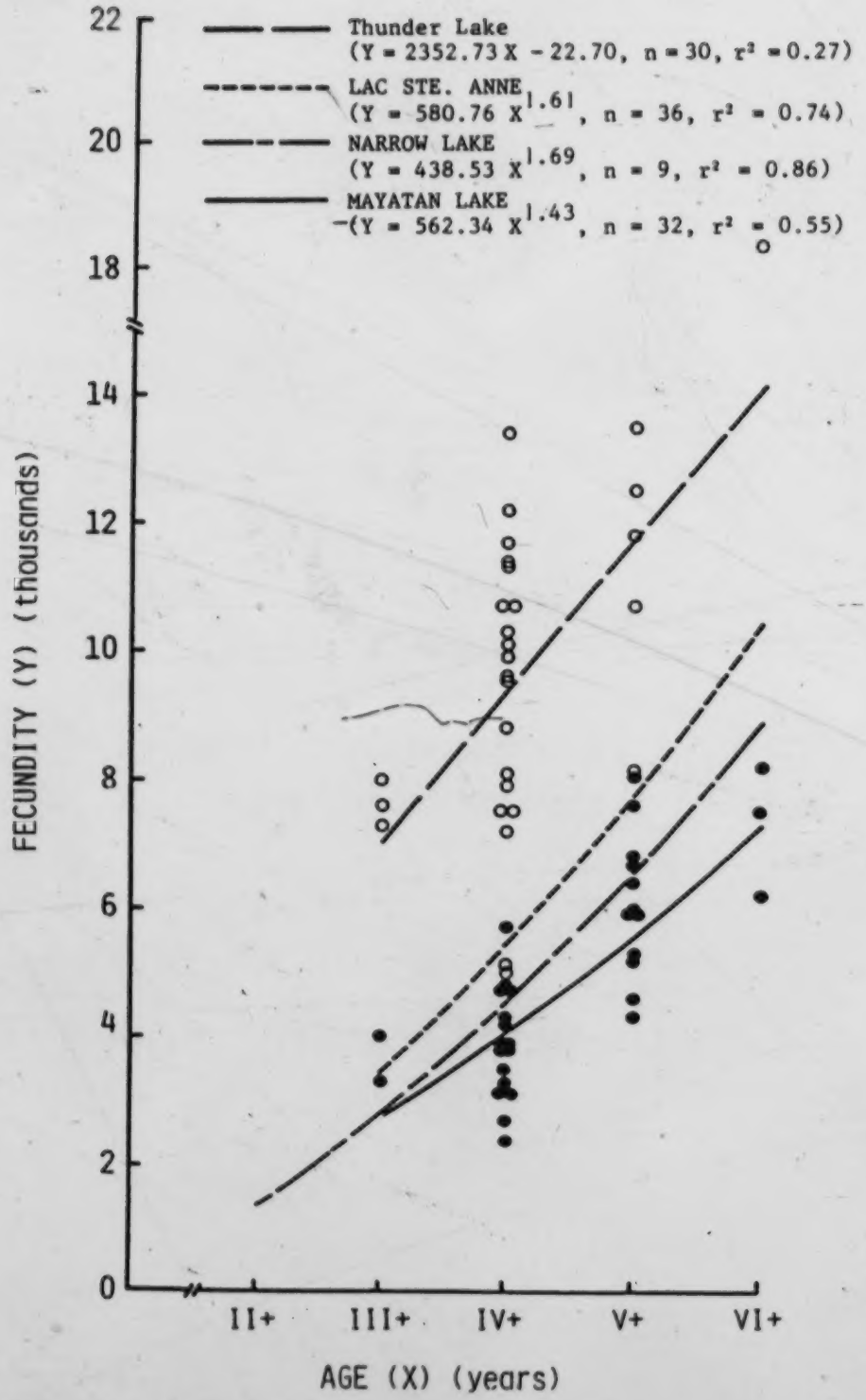

Fig. 2.7. Legend on the opposite page.

Table 2.5. Comparison of mean fecundity of various age groups of yellow perch collected from four Alberta lakes.

Lake	Mean Fecundity at Age[1]					
	II+	III+	IV+	V+	VI+	VII+
Mayatan	-	3,242	3,837	6,535	7,516	9,395
	-	(6)	(32)	(37)	(12)	(3)
Ste. Anne	-	3,617	5,300	7,831	10,863	15,088
	-	(12)	(19)	(38)	(19)	(2)
Thunder	-	7,552	9,501	11,327	14,128	-
	-	(10)	(36)	(14)	(4)	-
Narrow	1,747	2,477	3,295	7,406	8,935	-
	(1)	(2)	(1)	(4)	(1)	-

[1] Numbers in parentheses refer to the number of fish in each age group.

fecundity on total length, somatic weight, ovary weight, and age was done. The significance of each of the overall regressions and of each of the partial regression coefficients (slope) relating fecundity to each of the independent parameters is shown on Tables 13 to 16 of Appendix 1.

In the four-variable regression analyses for Mayatan Lake, Lac Ste. Anne, and Narrow Lake, neither length nor weight nor age contributed significantly to the predictive value of the equations. As expected, ovary weight was very highly correlated with fecundity in all the lakes. Only for the Thunder Lake data was age found to be significantly correlated, apart from ovary weight, with fecundity (Appendix 1, Table 17). When the non-significant total length and somatic weight were omitted from further analysis, and fecundity was regressed on ovary weight and age, the latter was significant only at the 5% level. Moreover, the multiple correlation coefficient of the fecundity on gonad weight and age relationship (0.98) was no different from that of the regression on ovary weight alone (0.98). Hence, there was no advantage gained by adding age to gonad weight in the predictive power of the equation. Thus, gonad weight at any one date was the best predictor of egg production in all the lakes.

To determine which of total length or somatic weight was a better predictor of fecundity, two-factor regressions of log fecundity on log total length and log somatic weight were done (Appendix 1, Tables 18 - 20). Somatic weight emerged as a better predictor of fecundity than total length in Mayatan Lake, Lac Ste. Anne, and Thunder Lake. When either length or weight were entered first in the two-variable equation for Narrow Lake, the F variance ratio was zero for the remaining variable, i.e., length and weight were equally robust in predicting fecundity in Narrow Lake. Thus, somatic weight was the second best predictor of egg production.

Age-length and age-weight interactions

When the effect of either total length or somatic weight was factored out, age had no further significant effect on the variation in fecundity (Appendix 1, Tables 21 - 28).

Age and size at sexual maturity

A total of 494 female yellow perch were collected from the four Lakes between 25 December 1982 and 15 March 1984 (Table 2.6). A female was classified as either sexually immature or mature based on the macroscopic descriptions of gonads given by Kesteven (1960). Immature females could be easily distinguished by their tiny thread-like ovary, found below the air bladder, which was characteristically translucent with no visible oocytes. Egg production was dominated by age V+ females in Mayatan Lake and Lac Ste. Anne, and IV+ females in Thunder Lake.

With the exception of one fish from Narrow Lake, no females matured at age II+. Age III+ seemed to be the most common age for the onset of sexual maturity for all the lakes except Mayatan where only 29% of III+ females were reproductively mature at that age. In Mayatan Lake most females (80%) were mature at age IV+ although a few (6%) remained immature at age V+. All females at age III+ or older from Narrow Lake, IV+ from Thunder Lake, IV+ from Lac Ste. Anne, and VI+ from Mayatan Lake were mature.

One-way analysis of variance for unequal sample sizes was used to test differences between lakes in the mean total lengths and mean somatic weights of mature and immature females within the same age class. This revealed that within Mayatan Lake, immature females were significantly shorter and lighter than mature females at ages IV+ and V+ (Tables 2.7 - 2.8). Mature age III+ females from Lac Ste. Anne were also significantly longer and heavier than similarly aged but immature females from the same lake. No such difference in size was found between immature and mature III+ females from Mayatan and Thunder Lakes. However, the absence of any significant difference may be due to the small sample sizes used.

D. DISCUSSION

Temporal changes in fecundity during gonad recrudescence

The present study presents direct evidence that in the yellow perch, the upper limit of fecundity is set early in oogenesis and that this maximum potential fecundity is modulated

Table 2.6. Number of mature and immature female yellow perch, collected from four Alberta lakes, at different ages.

Lake	Age (year) II+	III+	IV+	V+	VI+	VII+	VIII+
Mayatan[1]							
Mature	0	8 (29%)	76 (80%)	83 (94%)	48	16	1
Immature	1	20 (71%)	19 (20%)	5 (6%)	0	0	0
(Total)	1	28	95	88	48	16	1
Ste. Anne[2]							
Mature	0	16 (76%)	28	50	21	2	-
Immature	7	5 (24%)	0	0	0	0	-
(Total)	7	21	28	50	21	2	
Thunder[3]							
Mature	-	11 (79%)	41	17	4	-	-
Immature	-	3 (21%)	0	0	0	-	-
(Total)		14	41	17	4		
Narrow[4]							
Mature	1 (25%)	2	1	4	1	-	-
Immature	3 (75%)	0	0	0	0	-	-
(Total)	4	2	1	4	1		

[1] Samples were collected between 25 December 1982 and 17 January 1983, and between 8 October 1983 and 15 March 1984.

[2] Samples were collected between 18 January and 23 February 1984, and between 17 February and 12 March 1984.

Table 2.6. Continued ...

[3]Samples were collected in 22 February and 16 March 1984.

[4]Samples were collected in 23 February 1984.

Table 2.7. Comparison of mean total lengths of mature and immature female yellow perch within the same age groups using one-way analysis of variance.[1]

Lake	Age	Mature			Immature			F	Probability
		Number of Females	Total Length (cm) Mean	Range	Number of Females	Total Length (cm) Mean	Range		
Mayatan[2]	III+	8	15.59	14.1 - 15.1	20	15.12	13.2 - 17.0	1.61^{ns}	>0.05
	IV+	76	16.58	14.1 - 18.0	19	15.44	14.0 - 16.8	22.85	<0.001
	V+	83	18.26	16.0 - 23.0	5	16.56	16.0 - 17.1	10.73	<0.01
Ste. Anne[3]	III+	16	13.63	12.5 - 14.6	5	10.16	8.1 - 12.3	47.15	<0.001
Thunder[4]	III+	11	17.58	14.7 - 18.9	3	15.87	15.0 - 17.6	$3.63^{n.s.}$	>0.05

[1] *Ho:* there was no significant difference in the mean total lengths of mature and immature females belonging to the same age group.

[2] Samples were collected between 25 December 1982 and 17 January 1983, and between 8 October 1983 and 15 March 1984.

[3] Samples were collected between 18 January and 23 February 1983, and between 17 February and 12 March 1984.

[4] Samples were collected on 22 February and 16 March 1984.

Table 2.8. Comparison of mean somatic weights of mature and immature female yellow perch within the same age groups using one-way analysis of variance.[1]

		Mature			Immature				
		Number of	Somatic Weight (g)		Number of	Somatic Weight (g)			
Lake	Age	Females	Mean	Range	Females	Mean	Range	F	Probability
Mayatan[2]	III+	8	27.83	19.40-36.64	20	27.71	17.76-39.17	0.00[n.s.]	>0.05
	IV+	75	36.72	21.39-49.12	20	30.23	20.95-39.86	474.30	<0.001
	V+	82	50.09	32.67-98.90	5	37.88	34.79-42.00	5.78	<0.05
Ste. Anne[3]	III+	16	23.75	16.59-32.74	5	8.79	4.28-16.34	37.44	<0.001
Thunder[4]	III+	11	49.36	28.63-61.34	3	38.46	31.75-49.43	3.38[n.s.]	>0.05

[1] *Ho*: there was no significant difference in the mean somatic weights of mature and immature females belonging to the same age group.

[2] Samples were collected between 25 December 1982 and 17 January 1983, and between 8 October 1983 and 15 March 1984.

[3] Samples were collected between 18 January and 23 February 1983, and between 17 February and 12 March 1984.

[4] Samples were collected on 22 February 16 March 1984.

downward with the approach of spawning. This finding supports a similar theory by Hislop et al. (1978) and Robb (1982), whose work on the haddock, *Melanogrammus aegelfinus*, documented a temporal decline in fecundity. They proposed that such a decline in potential fecundity is correlated with adverse climatological factors operating during the later part of the maturation period of the oocytes. In the present study, the initial fecundity declined from October 1983 through to January 1984. Consequently, estimates made before January could lead to an overestimation of the actual fecundity. For a female with a total length of 19.0 cm, the potential fecundity declined by about 20% between October 1983 and March 1984. Whether this decline in fecundity occurs every year or only when the winter is unusually adverse has not yet been established. However, the lack of preovulatory atresia, the mechanism for limiting the initial fecundity, in the Eurasian perch (Jellyman 1980; Treasurer and Holliday 1981) may indicate that such decline does not happen every year.

Two explanations are given to account for this temporal decline in the fecundity of yellow perch. First, the occurrence of preovulatory atresia in half of the sections of Stage V and VI ovaries, collected in February and March, could explain the observed declined in fecundity with the approach of spawning (see Chapter 3). The extent of atresia in the sections could not be quantified because the histological technique required unsuitably small blocks of ovary tissue for fixing and embedding. The occurrence of atresia did not necessitate corrections in the estimates because atretic oocytes would almost certainly disintegrate in Gilson's fixative (Macer 1974).

How common is atresia in the yellow perch? The occurrence of atresia in perch from Mayatan Lake could not be extrapolated as a common phenomenon to the other three lakes because histological studies were not done on ovaries from these lakes. Although Jellyman (1980) and Treasurer and Holliday (1981) reported no preovulatory atresia in the Eurasian perch, it has been known to occur in a population of the species in Hamilton Lake in New Zealand (Graynoth, per. comm., cited by Jellyman 1980). Considerable atresia has been documented in the sturgeon, *Acipenser sturion*, where potential fecundity was reduced by 30 to 40% due to atresia (Badenko et al. 1973, cited by Treasurer and Holiday 1981). Similarly,

resorption of more than 50% of maturing oocytes has been documented in the brook trout, *Salvelinus fontinalis* (Vladykov 1956; Wydoski and Cooper 1966) and northern pike, *Esox lucius* (June 1970). Atresia is believed to be mediated by intensified and altered endocrine activity possibly as a result of stress (Ball 1969; Volodin et al. 1974). Factors such as restricted diet (Scott 1962; Hester 1964; Robb 1982), high population density (Warren 1973), and extreme fluctuations in water temperature and level (Hodder 1963; June 1970), are believed to increase resorption of oocytes.

Another possible explanation for the apparent decline in fecundity in the present work could be an artifact of the method used to determine fecundity. In spite of the distinct separation in size on microscopic examination between the resting oocytes and the larger developing oocytes by August (Fig. 3.11, Chapter 3), the small size of both types of oocytes made their separation by macroscopic examination in the October sample of ovaries difficult. This might have led to the inclusion of some large-sized resting oocytes with the developing ones which were counted for fecundity estimation. Data from Chapter 3 (Fig. 3.11) showed that overlap in the size of the resting and developing oocytes did not occur beyond July. However, as late as September, Treasurer and Holliday (1981) still detected overlap in the size of oocytes in the ovaries of the Eurasian perch. The inclusion of large-sized resting oocytes with developing oocytes, when estimating fecundity early in oogenesis, and the overlap in size between the two types of oocytes could both lead to an overestimation of fecundity.

The four studies which have reported fecundity for the yellow perch used animals collected at various times before the actual spawning time. Sampling ranged from many months before spawning (Sheri and Power 1969) to the actual spawning period (Tsai and Gibson 1971). The reliability of fecundity estimates early in oogenesis was questioned by Tsai and Gibson (1975) who felt that counting the large oocytes during the summer may lead to results different from those obtained by the usual method of counting maturing ova just prior to spawning.

Further studies should be directed to answering a number of questions. First, does the present finding of declining fecundity over time in the yellow perch indicate a strategy to

maximize the number of oocytes recruited into development in anticipation of optimum winter conditions, e.g., shorter ice-covered period? This would enable the fish to maximize reproductive output whenever environmental factors are favourable. Second, when adverse conditions prevail, do the yellow perch 1) sacrifice egg production by resorbing oocytes in order to maintain a certain body size that will ensure survival through the rigours of spawning and to carry a larger ovary for the next reproductive cycle? Or does the species opt to 2) sacrifice body weight by shunting energy into the ovaries? Under experimental conditions, the three-spined stickleback, *Gasterosteus aculeatus*, gives priority to egg production when faced with food shortage resulting in a significant decline in the weight and energy content of the soma (Wootton 1979). In contrast, field and laboratory observations in the winter flounder, *Pseudopleuronectes platessa*, indicate that they readily reduce the number of oocytes undergoing vitellogenesis, when food is scarce (Tyler and Dunn 1976). This allows them to maintain body weight so that when favourable conditions occur, they are able to produce a heavier ovary.

Comparison of fecundities of perch from four lakes

The results of this part of the study suggest an inverse relationship between growth rate and fecundity in yellow perch. Females from the slow-growing populations were more fecund than females of the same length from fast-growing populations. Consistent with the characteristics of an r-selected population (MacArthur and Wilson 1967), fish from Narrow Lake, where the abundance of yellow perch is possibly low because of very high mortality of the young of the year (Mackay, per. comm.), exhibited the highest length-specific fecundity when compared to similarly sized fish from the other lakes. Those from Mayatan Lake, where the population density was probably the highest, showed the lowest fecundity at a common length. Based on data collected from 1956 to 1961, Bagenal (1963, 1966) found that in the plaice, *Pleuronectes platessa*, fecundity was inversely related to population density. He believed that heavy fishing off the southwestern coast of Scotland from 1954 to 1956 reduced population density in some fishing grounds, and this led to decreased intraspecific competition

for food supply, which led to increased fecundity in the fish. Conversely, in places where the plaice were plentiful, like the North Sea (Simpson 1951) and southwest coast of Iceland (Bagenal 1960), the fish were less fecund. However, other factors may be involved aside from food resources and population density because fecundity did not increase in the Baltic plaice even though their abundance had been considerably reduced by exploitation (Bagenal 1966).

A possible role of age in the determination of fecundity should not be overlooked since the more fecund females from slow-growing populations are older at the same size than members of fast-growing populations. Reibisch (1899) and Franz (1910) (both cited by Bagenal 1969) proposed that the Baltic plaice, *Pleuronectes platessa*, were more fecund than the North Sea plaice because the former were older at the same size. Simpson (1951) restudied the plaice fecundity in the same areas, after the growth rates of the fish in both fishing grounds were about equal due to drastic changes in population density as a result of fishing. He found that the previously slow-growing Baltic plaice were still more fecund than the North Sea fish of the same length and age. He thus refuted Reibisch and Franz's hypothesis. The spawning experience of older fish may have an effect on fecundity because repeat spawners in the haddock, *Melanogrammus aegelfinus* (Hodder 1963) and capelin, *Mallotus villosus* (Winters 1971), are more fecund than first-time spawners of the same age and length. Gerking (1959), after reanalyzing data on the plaice, came to the conclusion that the effect of age may be masked by considerable variation in fecundity between and within populations.

Total length and fecundity

The regression of fecundity on total or fork length is the relationship most commonly used in examining and comparing egg production in perch populations (Thorpe 1977b). Although gonad weight and somatic weight are superior to total length in predicting egg production, total length is the most practical parameter to use because: 1) it is easily measured in the field and does not require that the fish be sacrificed; 2) it can adequately explain the observed variation in fecundity; and 3) it does not show any significant interaction with age in predicting fecundity. Moreover, samples collected at different times of the year

can be validly compared by using fecundity on length relationship because the magnitude of change in length with the approach of the spawning time is not as high as that of either somatic or gonad weight (Bagenal 1978). In the roach, *Rutilus rutilus*, bleak, *Alburnus alburnus* (Mackay and Mann 1969), catfish, *Clarias lazera* (Clay and Clay 1981), and summer flounder, *Paralichthys dentatus* (Morse 1981), body length is a better predictor of egg production than either weight or age.

Based on 124 observations from 62 marine and freshwater species, Wootton (1979) found that the values for the slope of fecundity on total length ranged from about 1.0 to 7.0 but clustered between 3.250 and 3.749. Simpson (1951) argued that the cubic relationship of egg number to length could be explained by the fact that the germinal epithelium is so convoluted that it fills the volume of the ovary. Fecundity is a function of ovary volume and thus the cube of the length.

The regression coefficient b (slope) of the fecundity-body length relationship for the four lakes studied, ranged from 3.685 (Mayatan Lake) to 3.822 (Thunder Lake). These slopes are higher than the 2.704 reported for yellow perch from Lake Ontario (Sheri and Power 1969, recalculated by Tsai and Gibson 1971) but lower than 3.999 for the Severn River in Maryland (Muncy 1962). The fecundities of the four Alberta lakes are compared with four other geographical locations in Fig. 2.8. The fecundity of a Narrow Lake female with a total length of 16.5 cm, is 2 and 3 times that of females from the Patuxent and Severn Rivers of the same length (fork lengths were adjusted to total lengths using the equation derived by Nakashima and Leggett 1975). If the estimate made by Sheri and Power (1969) for the yellow perch population from Lake Ontario is disregarded for possible overestimation since they used ovaries collected in the summer, and if adjustments are made so that all regressions of fecundity are made on total rather than fork length, it appears that Narrow Lake and Lac Ste. Anne females are more fecund than fish of the same length from populations reported in the literature.

The fecundity of fish from Thunder Lake was nearly the fourth power (3.822) of the total length. A similar phenomenon had been found in yellow perch from rich estuarine

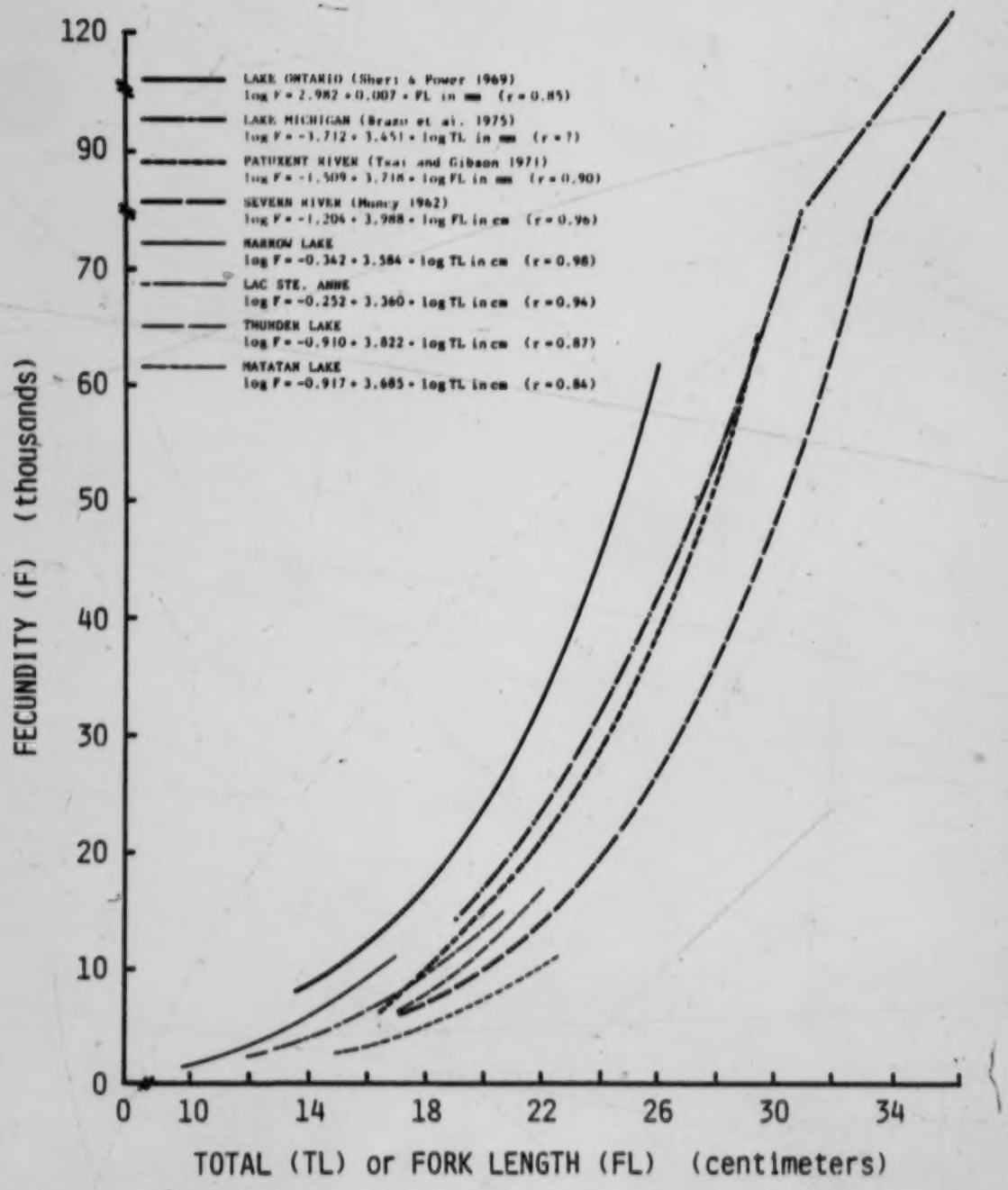
LAKE ONTARIO (Sheri & Power 1969)
log F = 2.982 + 0.007 • FL in mm (r = 0.85)
LAKE MICHIGAN (Brazo et al. 1975)
log F = -1.712 + 3.451 • log TL in mm (r = ?)
PATUXENT RIVER (Tsai and Gibson 1971)
log F = -1.509 + 3.718 • log FL in mm (r = 0.90)
SEVERN RIVER (Mumy 1962)
log F = -1.204 + 3.988 • log FL in cm (r = 0.96)
NARROW LAKE
log F = -0.342 + 3.584 • log TL in cm (r = 0.98)
LAC STE. ANNE
log F = -0.252 + 3.360 • log TL in cm (r = 0.94)
THUNDER LAKE
log F = -0.910 + 3.822 • log TL in cm (r = 0.87)
MATATAH LAKE
log F = -0.917 + 3.685 • log TL in cm (r = 0.84)
FECUNDITY (F) (thousands)
120
90
70
60
50
40
30
20
10
0
0
10
14
18
22
26
30
34
TOTAL (TL) or FORK LENGTH (FL) (centimeters)

Fig. 2.8. Comparison of fecundity of yellow perch from four Alberta lakes with four other geographical populations. The data points were omitted for clarity.

populations (Muncy 1962; Tsai and Gibson 1971). This had been correlated with the unusually heavy body weight and, hence, high slope of weight on length. Muncy (1962), who reported a slope of 3.999 for fecundity on fork length regression, found that the somatic weight on fork length relationship had a correspondingly high slope of 3.461. This is greater than that reported for the majority of the perch populations in North America - 3.015 for Lake Erie (Jobes, 1952), 3.054 for the Michigan lakes (Beckman 1946), and 3.112 for Lake Huron (El-Zarka 1959). However, the slope of somatic weight on total length relationship for the Thunder Lake females (2.830) is lower than all the above values. Clearly, other unidentified factors, possibly genetic, should be sought to explain the nearly quadruplicate relation of fecundity to length in Thunder Lake. The perch in Thunder Lake had been stocked in 1980 and were self-sustaining when sampled. The fish used for stocking were obtained from Clear Lake where their growth rate indicates stunting (Norris 1984).

Somatic and ovary weights and fecundity

The present work shows that somatic weight is a better indicator of egg production than total length. Previous reports on estuarine populations of the yellow perch showed a better correlation of fecundity with fork length than with somatic weight (Muncy 1962; Tsai and Gibson 1971). Perhaps in stunted slow-growing populations of yellow perch located near the limits of its geographic range, like those studied here, somatic energy reserves are very important in sustaining ovarian recrudescence over the winter period when the fish are presumably food limited. In the fertile estuarine environment, length may be more critical than weight in determining fecundity since length is directly related to the ability to compete for food which is easily available even during the winter period.

It has been argued that since weight is closely related to the condition of the fish, it should be a better indicator of egg production than length (Bagenal 1978). In the brook trout, *Salvelinus fontinalis* (Wydoski and Cooper 1966), yellow and Eurasian perch (Sheri and Power 1969; Treasurer 1981, present study), dolly varden, *Salvelinus malma* (Blackett 1973), groupers, *Epinephelus* spp. (Bouain and Siau 1983), and the clupeid *Pellonula afzeliusi*

(Ikusemiju et al. 1982), weight is better correlated to fecundity than length. In all the species named above, fecundity is linearly related to weight.

The data collected in the present study showed no decline in the number of oocytes per unit of body length as length increased. Previous investigations of the Eurasian perch have demonstrated an inverse relationship between relative fecundity and length or weight of the fish (Stehlik 1969; Federova and Vetkasov 1975; Jellyman 1980; Bregazzi and Kennedy 1982). It must be pointed out that all these studies included older, longer, and heavier perch than those collected in this study. Age-related degenerative changes in the ovaries of older and larger females may help explain this phenomenon of declining relative fecundity in large fish (Woodhead and Ellett 1969; Woodhead 1974).

In contrast to the findings of the present study, the perch literature reports semilogarithmic relationships between fecundity and ovary weight. This discrepancy could be attributed to the peculiarities of ovaries from the larger fish, 13.5 to 25.7 cm fork length in Lake Ontario (Sheri and Power 1969) and 19.0 to 35.7 in Lake Michigan (Brazo et al. 1975), used in previous reports. Connective tissue surrounding and permeating the ovaries increases disproportionately in larger fish (Hickling 1940; Bagenal 1978). Moreover, the eggs from big fish are larger than those from smaller ones resulting in lower length or weight specific fecundities than would be possible had egg diameter remained constant throughout the range of fish size. The latter has been observed in the Eurasian perch (Craig 1974; Bregazzi and Kennedy 1982).

Age and fecundity

There is no published information for the yellow or Eurasian perch on the effect of age on egg production independent of other body parameters. The multivariate regression analyses done in this work showed that variation in age makes no contribution to variation in fecundity beyond that predicted by differences in length or weight. Nevertheless, the effect of age should not be totally dismissed. Healey and Heard (1984) demonstrated clearly in the Chinook salmon, *Oncorhynchus tshawytscha*, that populations that spawn at an older age were

more fecund at a common length than populations that reproduce at a younger age.

Age and size at sexual maturity

In Lac Ste. Anne and Thunder Lake, sexual maturity at age III+ seemed to be common. This finding agrees with observations on the species from Saginaw Bay, Lake Huron (Hile and Jobes 1941), Lake Mendota (Hasler 1945), and Severn River, Maryland (Muncy 1962). Most females from Mayatan Lake did not mature until their fourth year of life. Scott and Crossman (1973) regard maturity at age IV+ as most common in North America. Female yellow perch from the Alberta lakes studied generally matured at smaller sizes than those from the lakes mentioned above.

It is possible that fish size is more important than age as a determinant of the onset of maturity as shown by the fact that mature age IV+ and V+ from Mayatan Lake and age III+ from Lac Ste. Anne were significantly larger than immature females belonging to the same age class. No previous work has reported differences in size between mature and immature females of the same age. Female yellow perch from Lake Michigan near Ludington, Michigan, the fastest growing among the populations in the five regions of the Great Lakes, generally mature at age II+ owing to their large size (Brazo et al. 1975). Fast-growing stocks of male Eurasian perch are known to mature at the end of their first year of life (Petrovski 1960, cited by Thorpe 1977b; Craig 1974).

The mean total lengths of females at the time of sexual maturity observed for Mayatan Lake (16.58 cm at age IV+), Lac Ste. Anne (13.63 cm at III+), and Thunder Lake (17.58 cm at III+) were shorter than the length reported for Saginaw Bay, Lake Huron (Hiles and Jobes 1941) and Lake Michigan (Brazo et al. 1975) which had a mean standard length at sexual maturity of 17.4 and 20.6 cm, respectively. Population-density-independent factors, such as extreme temperature, short growing period, and short breeding season, operate in these Alberta lakes, which are much further north in the geographic range of the yellow perch. These factors could possibly explain the early maturity at a far smaller size and higher fecundity at a common length than females from lower latitudes. While recognizing that

favourable growth may lead to early maturity, Alm (1952) reported that Eurasian perch found in very unfavourable environmental conditions are slow-growing and spawn at an early age. Similarly, Martin (1966) found that slow-growing plankton-feeding lake trout, *Salvelinus namaycush*, matured earlier than fast-growing fish-eating populations. Following a shift from a diet of yellow perch, which disappeared from the lake, to stocked cisco, *Coregonus artedii*, lake trout in Lake Opeongo in Ontario increased in growth rate but matured a year later than previously established (Martin 1970). This was a case of faster growth rate actually delaying sexual maturity.

E. CONCLUSIONS AND SUMMARY

(1) The present work shows that the annual maximum fecundity in the yellow perch is determined early in gonadal recrudescence. This potential fecundity is modulated downward by preovulatory atresia, which maybe brought about by adverse environmental factors operating during the maturation phase of the oocytes. Thus, counting oocytes early in oogenesis could lead to an overestimation of fecundity.

(2) Comparisons of the fecundity on total length regressions of females from four populations showed equivalent slopes but significantly higher elevations for slow-growing females than for fast-growing females at a common length. Hence, fecundity is inversely related to the growth rate of the fish.

(3) In the four lakes studied, fecundity is logarithmically related to total length, and linearly related to both somatic and ovary weights. As expected, ovary weight was the best predictor of fecundity. Although somatic weight generally had a stronger correlation with fecundity than total length, the latter was the most practical index of egg production. Fecundity was logarithmically related to age in all but one lake, where the relationship was linear. Consistent with previous reports, age is the poorest predictor of fecundity. Age contributes nothing significant to the explanation of variation in fecundity beyond that predicted by variation in either total length or somatic weight.

(4) Female yellow perch from the Alberta lakes studied were sexually mature at shorter lengths and were more fecund at a common length than females from more southerly populations.

(5) Mature females were generally larger both in length and weight than immature females of the same age. Beyond the first year of life, size rather than age appears to be most important in determining the onset of reproductive maturity.

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III. HISTOLOGY OF OVARIAN RECRUDESCENCE IN THE YELLOW PERCH (*Perca flavescens* Mitchill) FROM AN ALBERTA LAKE

A. INTRODUCTION

Although the early development (Mansueti 1964), life history (Muncy 1962), and reproductive biology (Harrington 1947; Collette et al. 1977; Hokanson 1977; Thorpe 1977a, 1977b) of the yellow perch, *Perca flavescens* (Mitchill), are well documented, no work has been done on the histology of ovarian recrudescence. Early microscopic studies on the yellow perch egg and ovary were superficial, being limited to simple descriptions of structures. Ryder (1887) noted that the egg membrane (chorion) in the yellow perch consisted of an inner layer, which he considered homologous to zona radiata, a middle layer, which he described as distinctively thick, elastic, and radiated in appearance, and an outer adhesive layer. He also described the presence of a pore canal on the surface of the egg which leads to the micropyle. Mansueti (1964) agreed with Ryder's description of three layers of the chorion. She observed that unfertilized eggs contain diagnostic lipid droplets that impart a dark-yellow colour to them. Parker (1942) observed that unlike many teleosts, the yellow perch have only one ovary which lies on the midline of the body cavity below the swim bladder and above the digestive tract.

Before the publication of Treasurer and Holliday's (1981) paper, there was also a paucity of data on the histology of the ovarian cycle in the Eurasian perch, *Perca fluviatilis* (L.). Previous studies on the Eurasian perch had been limited to evaluation of gonad development either in terms of macroscopic description of the different stages of maturity (Kesteven 1960) or use of gonadosomatic index (gonad weight as a percentage of somatic weight) (Le Cren 1951; Craig 1974).

Yellow perch are annual spawners that lay all their eggs at one time during periods of rising water temperature in the spring (Hokanson 1977). Their eggs are group-synchronous in development. In species with group-synchronous development, two populations of oocytes can be differentiated at one time. A clutch consisting of oocytes which develop synchronously,

and another consisting of smaller oocytes at different stages of development from which the former clutch is recruited (Wallace and Selman 1981). Synchronous development permits the study of the time course of oogenesis by sampling females from a population during ovarian recrudescence. The present study takes advantage of this feature of yellow perch.

The growth of the ovary in *Perca* spp. occurs during the coolest months of the year when somatic growth is minimal. Based on studies in the Eurasian perch (Le Cren 1951; Koshelev 1963) and yellow perch (Brazo 1973, cited by Hokanson 1977), the reproductive cycle is as follows: After ovulation in spring, the ovaries undergo a transitional stage of maturity, which is characterized by resorption of residual eggs from the previous spawning. During the next stage, lasting about 2 1/2 months from mid June to August, the primary oocytes enter a phase of active vitellogenesis with minimal change in size. Further growth of the oocytes, accompanied by vacuolation, is observed from early September to late October. Fat and yolk deposition begin in November. Growth and maturation of the oocytes continue until spawning during the spring of the following year.

Although the histology of ovarian development may be similar in the two perch species, the author felt that a separate study of the yellow perch was warranted particularly of a population from a northern location which expriences shorter growing season and longer winter than the Eurasian perch populations previously studied.

The objectives of the present study were to describe histological changes in the ovary of the yellow perch during recrudescence and to determine how these were related to changes in gonadosomatic index. Emphasis is directed toward the 1) determination of the timing of recruitment; 2) identification of the developmental stage at which recruitment occurs; and 3) the presence of preovulatory oocyte degeneration that could explain the observed decline in fecundity towards the spawning season (see Chapter 2).

B. MATERIALS AND METHODS

Yellow perch were captured by the use of Windermere traps (Worthington 1950) and angling in Mayatan Lake (53° 30' N, 114° 15' W) from 15 May 1983 to 16 March 1984. At each sampling date, ovaries were collected for histological studies from six females ranging in total length from 17.0 to 20.0 cm. The length range was deliberately kept small because egg size is known to be positively correlated with body size in the Eurasian perch (Craig 1974; Bregazzi and Kennedy 1982).

Portions measuring 0.5 cubic cm in size from the anterior, middle, and posterior regions of the ovary were fixed immediately in the field in 2.5% glutaraldehyde in isotonic phosphate-buffered sucrose solution (pH 7.4) at 4° C for at least 24 hr. This was followed by four washings in isotonic phosphate-buffered sucrose solution and by storage in 70% ethyl alcohol. After dehydration in absolute ethyl alcohol, the samples were embedded in JB4, a plastic resin manufactured by Du Pont Company, Newtown, Connecticut. Sections were subsequently cut with glass knives at 3.0 μm, stained in polychrome I, and counterstained in polychrome II (Mackay and Mead 1970).

The stage of maturity was determined for the six ovaries using the descriptive method developed by Kesteven (1960). An ovary showing the maturity stage most common to the ovaries was then selected for oocyte measurements. A total of 100 oocytes were then measured at random from one representative ovary. The diameters were measured on the longest axis since the oocytes were not perfectly spherical. Only those oocytes sectioned through the nuclei were measured. The extent of ovarian development was expressed as the gonadosomatic index (gonad weight as a percentage of the somatic weight).

C. RESULTS

Table 3.1 shows the mean diameter, and 95% confidence limits for oocyte diameters at each maturity stage. Oogonia were present in ovaries at all stages of maturity but they were measured only in Stage II. Their size appeared to remain constant throughout the study.

Table 3.1. Mean diameter (μm) of resting and developing oocytes at different maturity stages of the ovary for yellow perch collected from Mayatan Lake, Alberta, on ten different dates.

Sampling Date	Maturity Stages of the Ovary[1]	Resting Oocytes: Mean Diameter ± 95% C. L.[2]	n	Developing Oocytes: Mean Diameter ± 95% C. L.	n
1983					
15 May	IID (Maturing virgin)[3]	160.2 ± 15.2	100	not observed	
15 May	IIR (Recovering mature)[4]	161.7 ± 6.1	100	not observed	
27 June	III (Developing early)	136.0 ± 6.2	100	263.8 ± 5.9	100
27 July	III (Developing early)	144.0 ± 5.6	95	262.8 ± 4.2	96
14 August	III (Developing early)	120.2 ± 8.8	100	373.3 ± 5.7	100
18 October	IV (Developing late)	131.0 ± 4.5	100	812.7 ± 9.0	100
5 December	IV (Developing late)	130.5 ± 4.7	100	832.4 ± 7.8	100
1984					
28 January	IV (Developing late)	137.8 ± 6.4	100	863.6 ± 8.7	100
28 February	V (Gravid)	140.2 ± 6.3	100	956.4 ± 14.2	100
16 March	VI (Spawning)	144.5 ± 5.9	100	1,004.2 ± 15.3	100

[1] The maturity stages of the ovary were designated according to Kesteven (1960)

[2] C. L. = confidence limits

[3] Oogonia were measured only in Stages IID and IIR. (Stage IID: mean diameter = 57.0; 95% confidence limits = 7.9; n = 20)

[4] (Stage IIR: mean diameter = 57.3; 95% confidence limits = 8.7; n = 20)

There was no difference observed in the histology of the sections taken from the anterior, middle, and posterior regions of the ovaries.

Stage IID: Maturing virgin

Maturing virgins, identified by their tiny thread-like translucent ovaries with no visible oocytes (Kesteven 1960), were found among the fish collected in May. Longitudinal sections of the ovary of maturing virgins showed advanced organization characterized by regularly arranged lamellae of oocytes that were separated by gaps of 20 to 40 μm (Fig. 3.1). Connective tissue enveloped and continued, together with blood vessels, into the center of each lamella. Each lamella was partitioned along its longitudinal axis into two bands, each one oocyte thick.

Three types of cells - germ cells (gc), oogonia (o), and primary oocytes (po) - could be distinguished along the external edge of the lamellae (Fig. 3.1). The germ cells, 4 to 7 μm in diameter, were found clustered along the inner margin of each band close to the blood vessels. These cells contained minimal cytoplasm which stained lightly basophilic, and their nuclei were centrally located. Oogonia, derived by mitotic divisions of the germ cells, measured 33 to 85 μm in diameter. Their light pink nuclei, 17 to 34 μm across, contained one or two nucleoli occupying a variable position in the chromatin network. The primary oocytes were larger, 80 to 250 μm across, with deep purple cytoplasm and light pink nuclei (48 to 85 μm diameter) containing up to 24 nucleoli. In the smaller primary oocytes, the nucleoli were restricted in their distribution towards the center of the nucleus. In the larger oocytes, the nucleoli were arranged around the inner aspect of the nuclear envelope which was typical of the perinucleolar stage. Each oocyte was bounded by a layer of thecal cells each with dark flattened nucleus.

Stage IIR: Recovering Mature

Stage IIR ovaries were identified in the majority of the females collected in May. Internal organization characterized by lamellae of oocytes were similar to Stage IID (Fig. 3.2)

Fig. 3.1. Stage IID (maturing virgin). A longitudinal section through the ovary of a maturing virgin showing regularly arranged lamellae. The primary oocytes (po) can be easily distinguished by their larger size and numerous nucleoli (arrows) at the edge of the nucleus (n) from the smaller oogonia (o). Note that there are fewer but larger nucleoli in the oogonia than in the primary oocytes. The ovary was collected on 15 May 1983. (gc, germ cell)

Fig. 3.2. Stage IIR (recovering mature). A longitudinal section through the ovary of a recovering mature female showing dilated blood vessels (bv) and a more extensive connective tissue matrix (ct) and smooth muscle (sm) than in the ovary of a virgin (Stage IID). Dark basophilic extrafollicular bodies (eb), interspersed among the primary oocytes (po) and oogonia (o), are common at this stage. The ovary was collected on 15 May 1983.

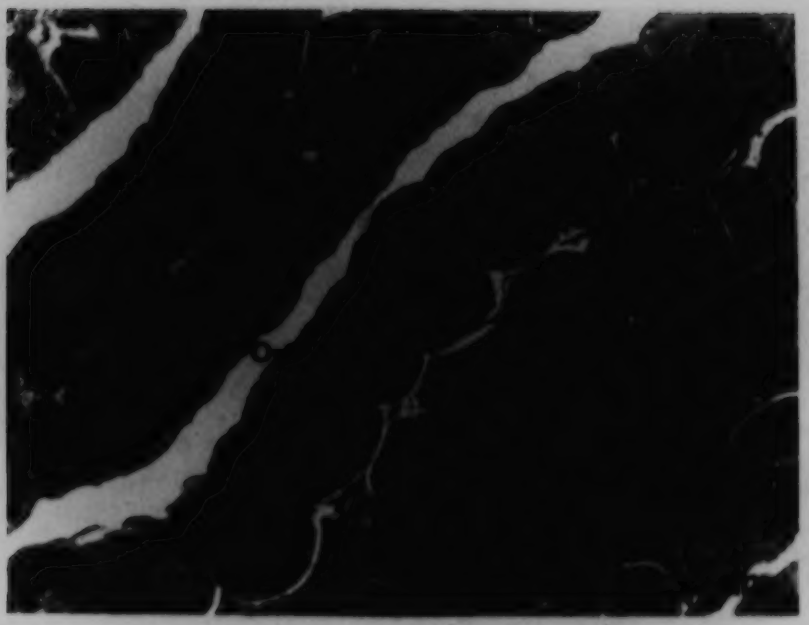

Fig. 3.1

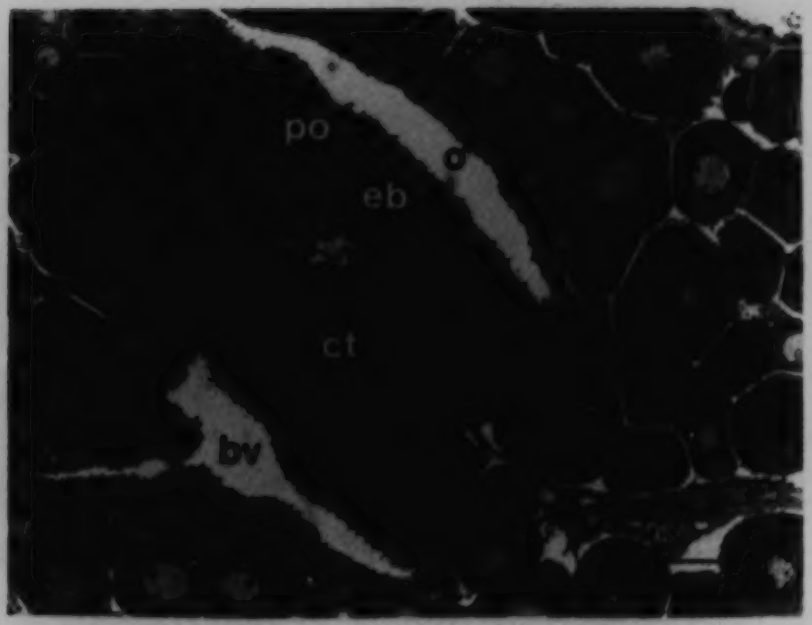

Fig. 3.2

described by Kesteven (1960). However, the following differences could be observed: (1) the connective tissue matrix of the lamellae was more extensive; (2) the blood vessels that supply the lamellae had thinner walls and were dilated; and (3) the numerous dark-staining extrafollicular bodies (eb) were scattered among the oocytes. In most sections examined, the primary oocytes showed a theca externa (te), a granulosa (g), and partial vacuolation of the cytoplasm indicative of the onset of endogenous vitellogenesis (Fig. 3.3).

Both Stages IID and IIR were seen in sections of ovaries collected in May, just after spawning.

Stage III: Developing (early)

Sections of ovaries obtained in June were at Stage III following Kesteven's (1960) method of identification. Recruitment had started at this stage giving rise to a bimodal distribution of oocyte diameters corresponding to developing (do) and resting oocytes (ro) (Fig. 3.4). The larger developing oocytes (do), 190 to 320 μm in diameter, with many dark-staining yolk vesicles, could easily be distinguished from the smaller light-staining resting oocytes (ro). The nucleus of the developing oocytes, 54 to 122 μm across, stained light pink with several nucleoli occupying the periphery. The cytoplasm stained light purple and contained deeply basophilic to slightly acidophilic yolk vesicles (yv) ranging in diameter from 3 to 34 μm. The smaller deep staining vesicles were restricted to the more peripheral cytoplasm and formed a ring around the larger vesicles. No yolk vesicles were observed in the cytoplasm immediately around the nucleus.

The external layer of the follicle (Fig. 3.5) was bounded by a theca externa composed of squamous-like cells with flattened nuclei. Internal to the theca externa was a layer of cuboidal granulosa cells 3 to 10 μm in diameter. The chorion, a secondary membrane laid down by the granulosa, showed two layers: an inner zona radiata and an outer tunica propria (tp). The zona radiata (zr), 1 to 3 μm thick, typically stained intense pink. Less distinct was the loose network of material that comprised the tunica propria.

Fig. 3.3. A primary oocyte (po) from an ovary in a more advanced stage of recovery (Stage IIR) showing a theca externa (te) and a granulosa layer (g). The larger primary oocytes also show vacuoles (v) which are indicative of endogenous vitellogenesis. The ovary was collected on 15 May 1983. (bv, blood vessel; n, nucleus; ns, nucleolus)

Fig. 3.4. Stage III (developing early). A dichotomy in the size of developing (do) and resting oocytes (ro) was first seen at this stage. Numerous intensely basophilic to slightly acidophilic yolk vesicles (yv) fill the cytoplasm except the region immediately around the nucleus (n). The ovary was collected on 27 June 1983. (o, oogonium)

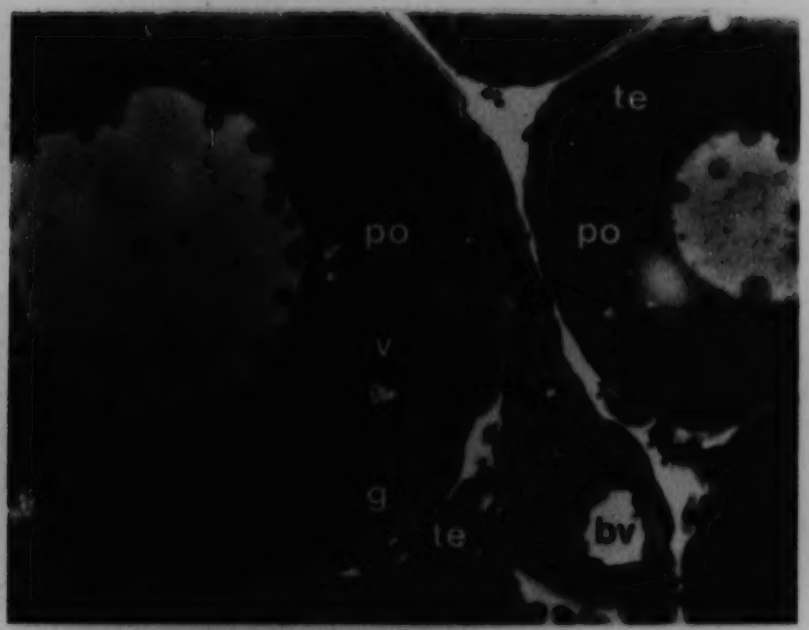

Fig. 3.3

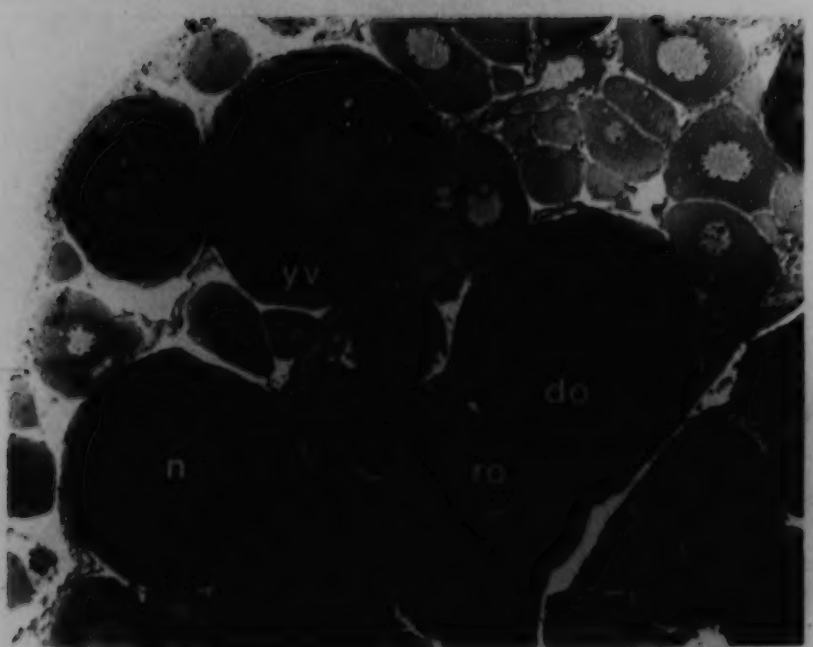

Fig. 3.4

The nucleus and ooplasm constituted 96.2% of the mean total oocyte volume at this stage. The remaining volume was accounted for by the two layers of the chorion.

Stage-III ovaries from fish collected in August showed a further increase in the size of the developing oocytes (290 to 440 μm diameter) due to continued accumulation of yolk vesicles. More yolk vesicles with a wider range in size, 5 to 51 μm, filled the cytoplasm, even the region immediately around the nucleus which was previously devoid of vesicles. The nucleus and ooplasm contributed 96.7% of the mean total oocyte volume. Hence, from June to August, the chorion made no substantial contribution to the increase in total oocyte volume.

Resting oocytes were small ranging from 80 to 220 μm across. They were found, together with oogonia and germ cells, clustered between the developing oocytes. The majority of the resting oocytes were at the perinucleolar stage. The cytoplasm was moderately basophilic and exhibited no yolk vesicles nor granulosa layer. However, a recognizable primary theca enveloped each resting oocyte.

Stage IV: Developing (late)

Figure 3.6 shows the developing oocytes n October. They were 770 to 970 μm in diameter, and could be distinguished from those of the early developing phase. The deeply basophilic yolk vesicles, now aptly termed cortical alveoli (ca), had been displaced peripherally by yolk granules (yg), which were formed by exogenous (true) vitellogenesis. The circular yolk granules were 6 to 31 μm across and did not take up stain. Scattered among the yolk granules were clear spherical structures, measuring 3 to 70 μm, which could have previously been occupied by lipid droplets.

The chorion, 27 to 108 μm wide, had enlarged significantly and three layers could now be seen. The inner zona radiata, 7 to 10 μm wide, stained an intense pink and showed radial striations. The middle chorion (mc) was widest ranging from 17 to 85 μm and stained pink. There were no perceptible changes in the granulosa and theca externa cells. The middle chorionic layer had thickened significantly so that the entire chorion accounted for 28.5% of

Fig. 3.5. Advanced Stage III oocytes. The advanced developing oocytes (do) in ovaries collected on 14 August 1983 show a distinct external membrane consisting of 1) an outer theca externa (te), composed of squamous-like cells, and 2) an inner granulosa layer (g) of cuboidal cells. The faintly visible tunica propria (tp) is the only layer of the chorion that is present at this stage. The smaller yolk vesicles (yv) are more intensely basophilic than the larger yolk vesicles. (n, nucleus)

Fig. 3.6. Stage IV (developing late). The deeply basophilic yolk vesicles, aptly called cortical alveoli (ca) at this stage, have been displaced to the periphery of the cytoplasm by the yolk granules (yg). The presence of yolk granules and vacuoles (v), possibly occupied by lipid globules previously, is an indication of exogenous vitellogenesis. Note that the zona radiata (zr) and the middle chorion (mc) are now distinct. The ovary was collected on 18 October 1983. (bv, blood vessel; do, developing oocyte; ro, resting oocyte)

Fig. 3.5

Fig. 3.6

the mean total oocyte volume.

Germ cells, oogonia, and resting oocytes formed clusters between the developing oocytes.

Stage V: Gravid

By February, the developing oocytes had again increased in size. They were 810 to 1090 μm in diameter, and the granules were more basophilic than earlier stages (Fig. 3.7). Many circular structures, 3 to 90 μm across, possibly containing lipid droplets, were found scattered among the yolk granules. The deeply basophilic cortical alveoli, restricted to the inner margin of the zona radiata, could be easily distinguished from the yolk granules. The nuclei were still identifiable with several distinct nucleoli. The chorion had a mean thickness of 120 μm (cf. 43 μm in Stage IV). The middle chorion was the widest (mean 118 μm) and most conspicuous of the three chorionic layers at this stage. The chorion constituted 58.1% of the mean total oocyte volume at this stage.

Stage VI: Spawning

This stage of development was typical of the ovaries collected in March. Further increase in the diameter of the developing oocytes, 820 to 1100 μm, characterized this stage (Fig. 3.8). The thickening of the middle chorion to a mean of 155 μm (cf. 118 μm in Stage V) contributed largely to the growth of the developing oocytes (Fig. 3.9). The thickened chorion contributed 67.8% of the mean total oocyte volume. The blood vessels supplying the follicles were greatly distended. The histology of this stage was otherwise very similar to that of Stage V.

Preovulatory atresia

All the stages were examined for evidence of preovulatory atresia of oocytes. Four of the 6 Stage V and 3 of the 6 Stage VI ovaries showed some oocytes (at) undergoing atresia (Fig. 3.10). The chorion of these oocytes was degenerating and the contents of the cytoplasm

Fig. 3.7. Stage V (gravid). The deeply basophilic cortical alveoli (ca) line the inner margin of the zona radiata (zr). The centrally located yolk granules (yg) have increased in size significantly. The middle chorion (mc) is the most conspicuous of the three chorionic layers. Ovary was collected on 28 February 1984. (bv, blood vessel; do, developing oocyte; ro, resting oocyte)

Fig. 3.8. Stage VI (spawning). Growth of the developing oocytes (do) is primarily due to the increase in the amount of yolk granules (yg) in the cytoplasm and the thickening of the middle chorion (mc). The ovary was collected on 15 March 1984. (n, nucleus; ro, resting oocyte; zr, zona radiata)

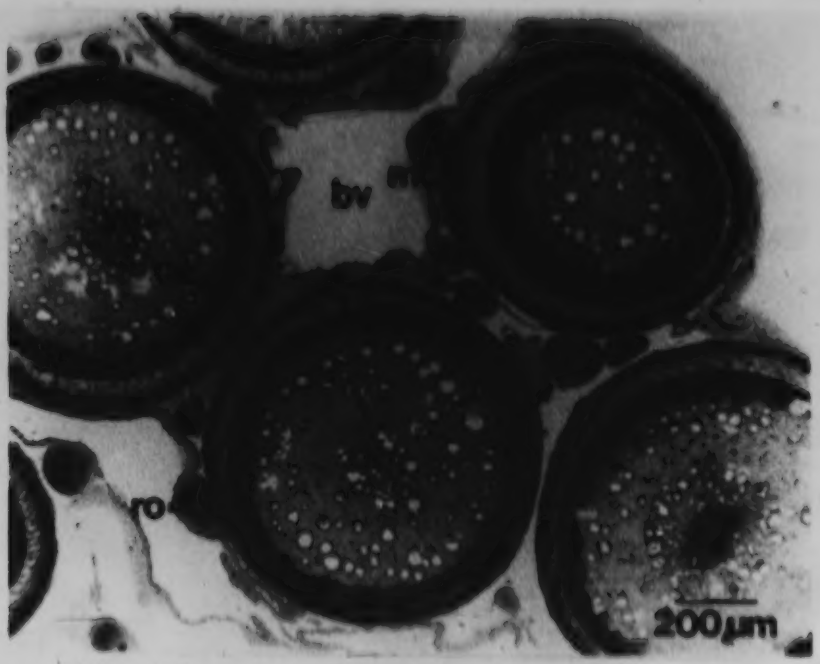

Fig. 3.7

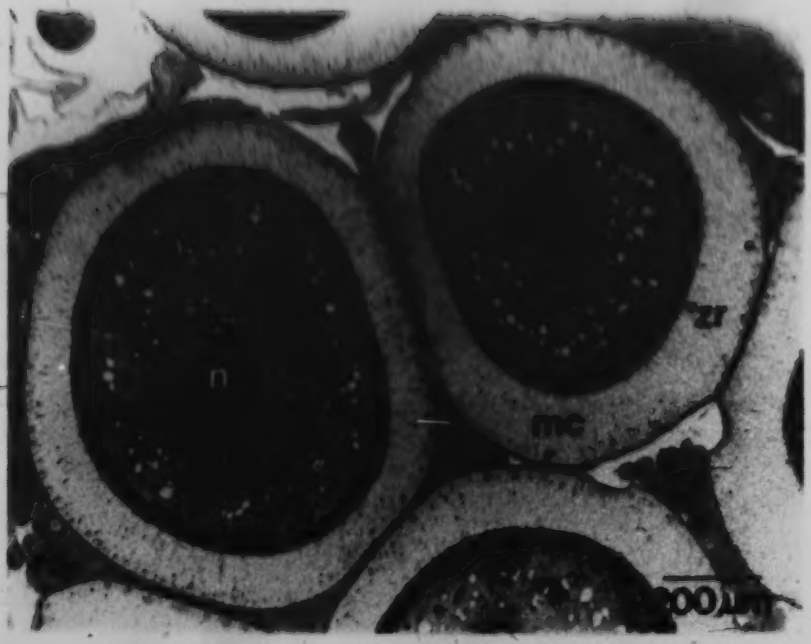

Fig. 3.8

Fig. 3.9. The chorion showing the three layers: zona radiata (zr), middle chorion (mc), and tunica propria (tp). The oocyte was sectioned from a Stage VI ovary collected on 16 March 1984. (ca, cortical alveolus; g, granulosa; ro, resting oocyte)

Fig. 3.10. Preliminary stage of preovulatory atresia found in a Stage V ovary collected on 28 February 1984. The breakdown of the chorion is very distinct. (at, atretic oocyte; do, developing oocyte; mc, middle chorion; ro, resting oocyte)

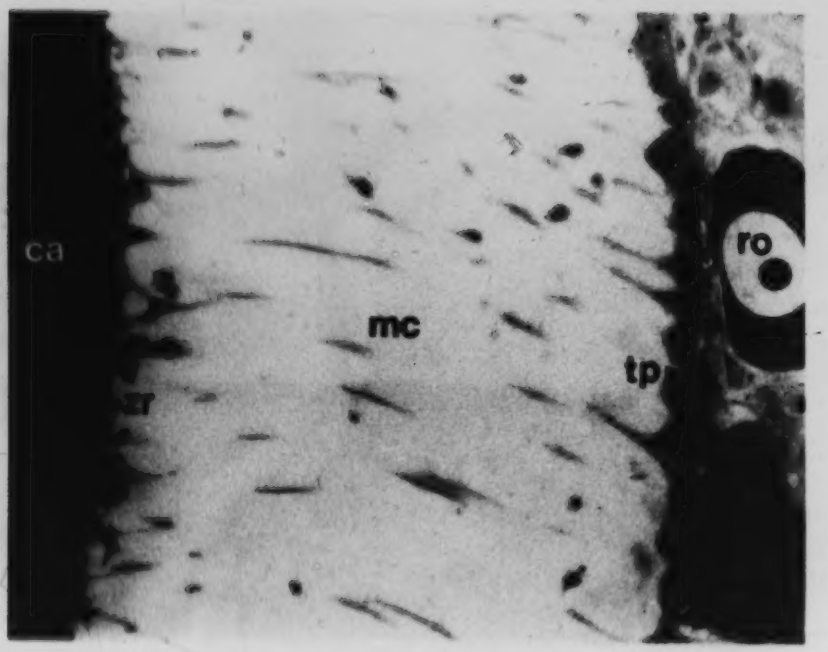

Fig. 3.9

Fig. 3.10

were being extruded at points where the chorion was broken. A more advanced state of oocyte degeneration was not found.

Oocyte diameter and volume

Figure 3.11 illustrates the size distribution of oocytes at various times between 8 October 1983 and 15 March 1984. A bimodal distribution in oocyte diameter was evident as early as Stage III in late June. This coincided with the appearance of vitellogenic oocytes, an indication of recruitment. By the end of the study the developing oocytes had increased 6.2 times in diameter.

Figure 3.12 shows that the diameter of the oocytes increased rapidly from late July to early October, and from late January to mid March. These rapid increments in oocyte diameter could be correlated with rapid increase in ooplasmic volume from July to October, and with rapid thickening of the chorion, particularly the middle layer, from January to March (Fig. 3.13). From July to October, the ooplasmic volume increased by 90.8 times. But it remained almost unchanged from October to March varying by only 6.6% each month from the mean of 1.79 cubic mm. Thus the continued growth in oocyte volume during the months when the lake was ice-covered was primarily due to the thickening of the chorion. From late June to mid March the chorion accounted for from 3.8 to 67.8% of the total oocyte volume.

Gonadosomatic index (GSI)

Figure 3.14 shows that the trend in ovary development expressed as the gonadosomatic index. There was little increase in the GSI from mid May to mid August. From mid August to late February just before spawning, there was a rapid increase in the GSI. There was however little change in GSI from February to mid March.

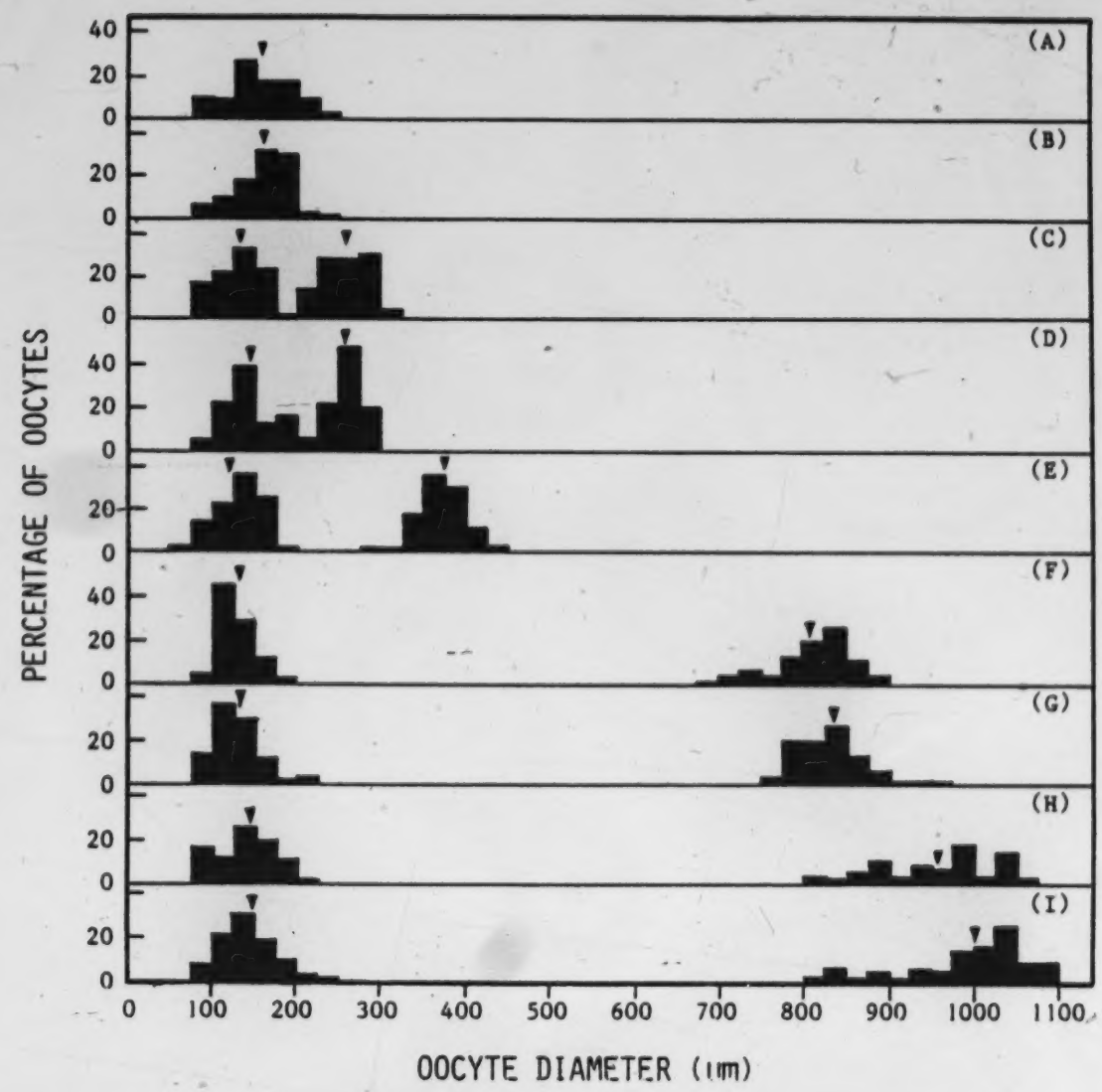

Fig. 3.11. Frequency distribution of oocyte diameter for each maturity stage of the ovary in the yellow perch. The oocytes are grouped in 25 um size classes. The arrows indicate the mean diameter of the oocytes. Each histogram represents measurements of 95 to 100 oocytes from one fish. Fish used ranged from 17.2 to 17.5 cm in total length. (A) Stage IID (maturing virgin), 15 May 1983. (B) Stage IIR (recovering mature), 15 May 1983. (C) Stage III (developing early), 27 June 1983. (D) Stage III (developing early), 27 July 1983. (E) Stage III (developing early), 14 August 1983. (F) Stage IV (developing late), 18 October 1983. (G) Stage IV (developing late), 5 December 1983. (H) Stage V (gravid), 28 February 1984. (I) Stage VI (spawning), 16 March 1984.

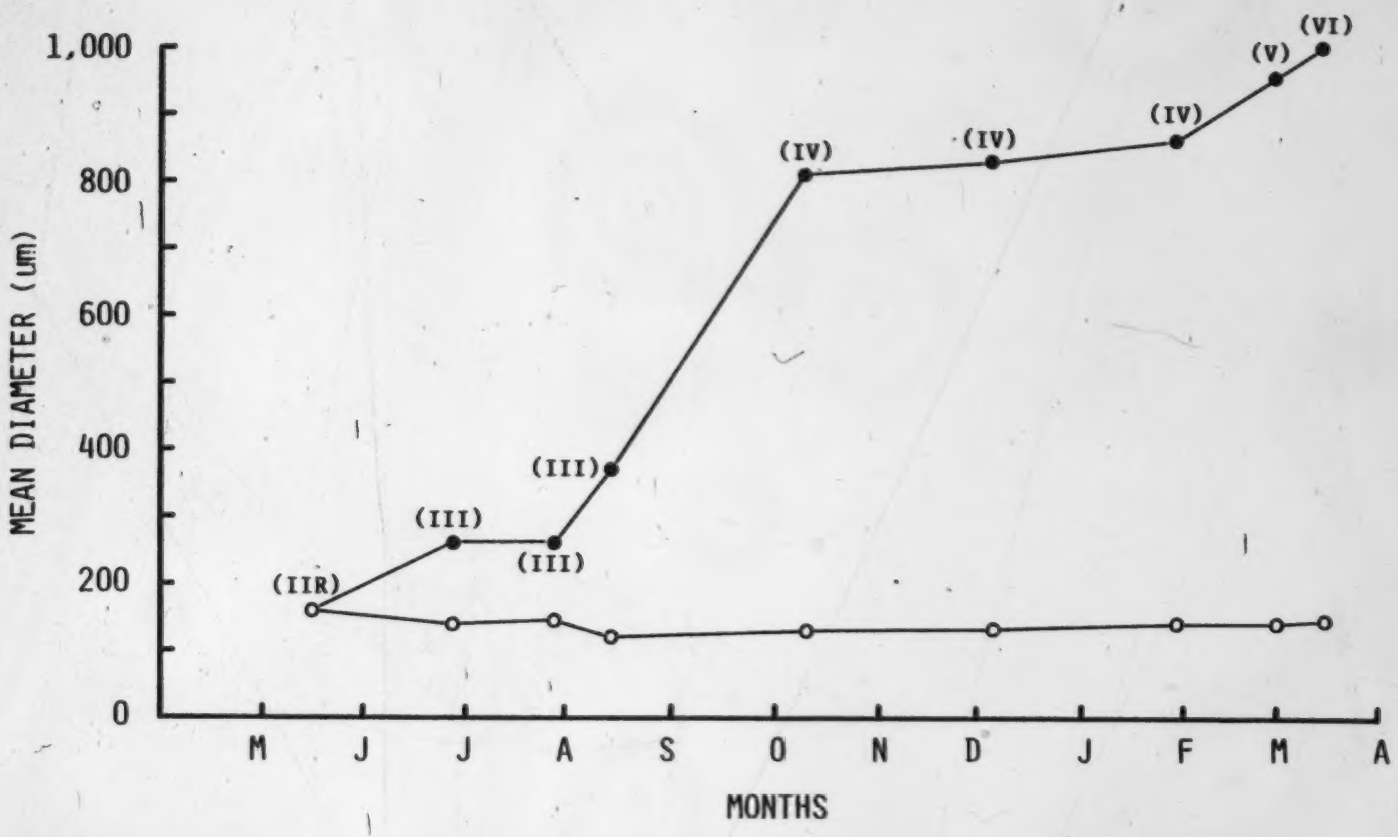

Fig. 3.12. Mean diameter of resting (open circles) and developing oocytes (solid circles) in female yellow perch collected from Mayatan Lake between 15 May 1983 and 16 March 1984. The Roman numerals in parentheses refer to the maturity stage of the ovary according to Kesteven (1960).

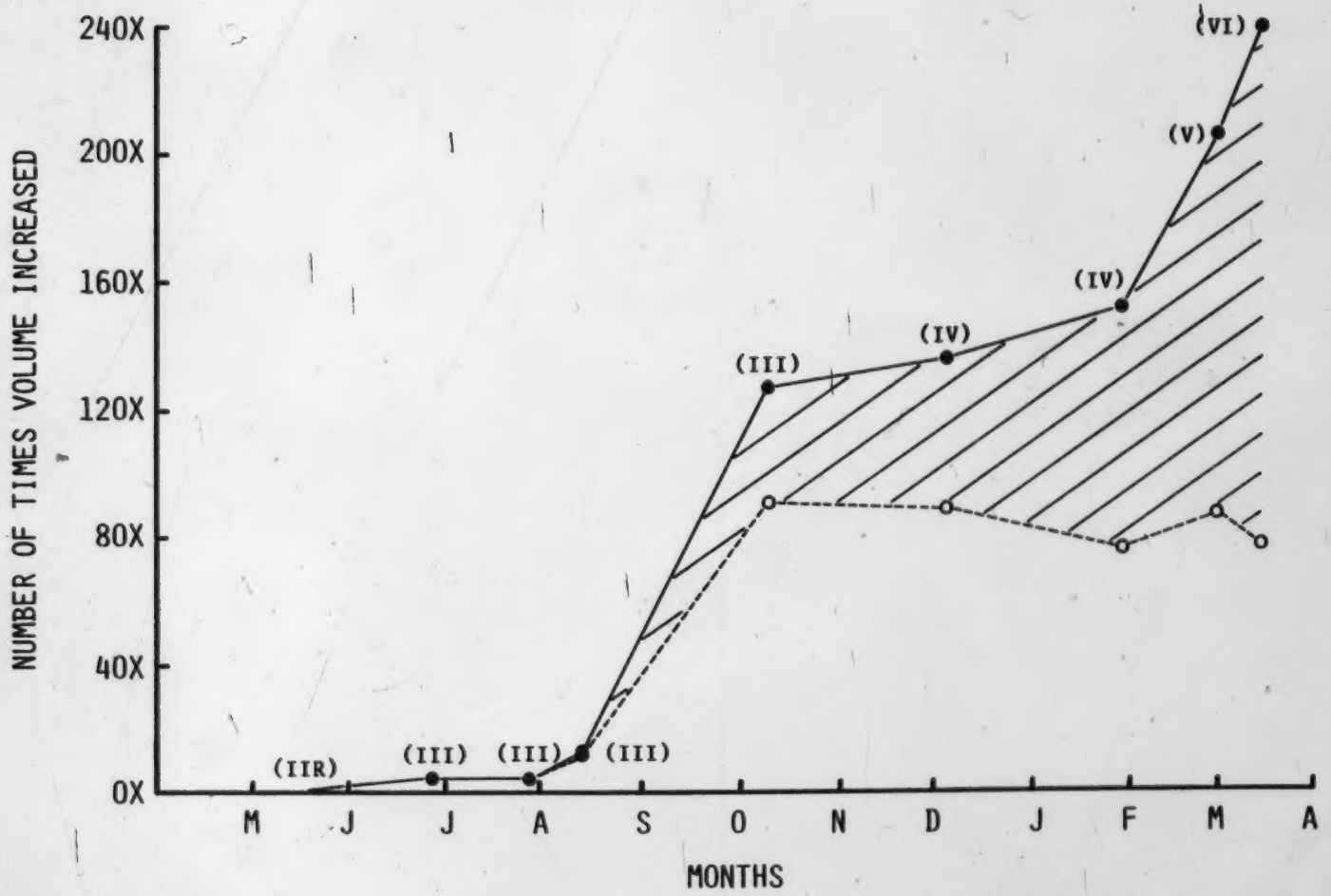

Fig. 3.13. Number of times the developing oocytes increased in mean total volume (solid circles) in yellow perch collected from Mayatan Lake between 15 May 1983 and 16 March 1984. The open circles represent the increase in total oocyte volume minus the chorion. The shaded area corresponds to the contribution of the thickening chorion to the growth of the oocytes. The Roman numerals in parentheses are the maturity stages of the ovary according to Kesteven (1960).

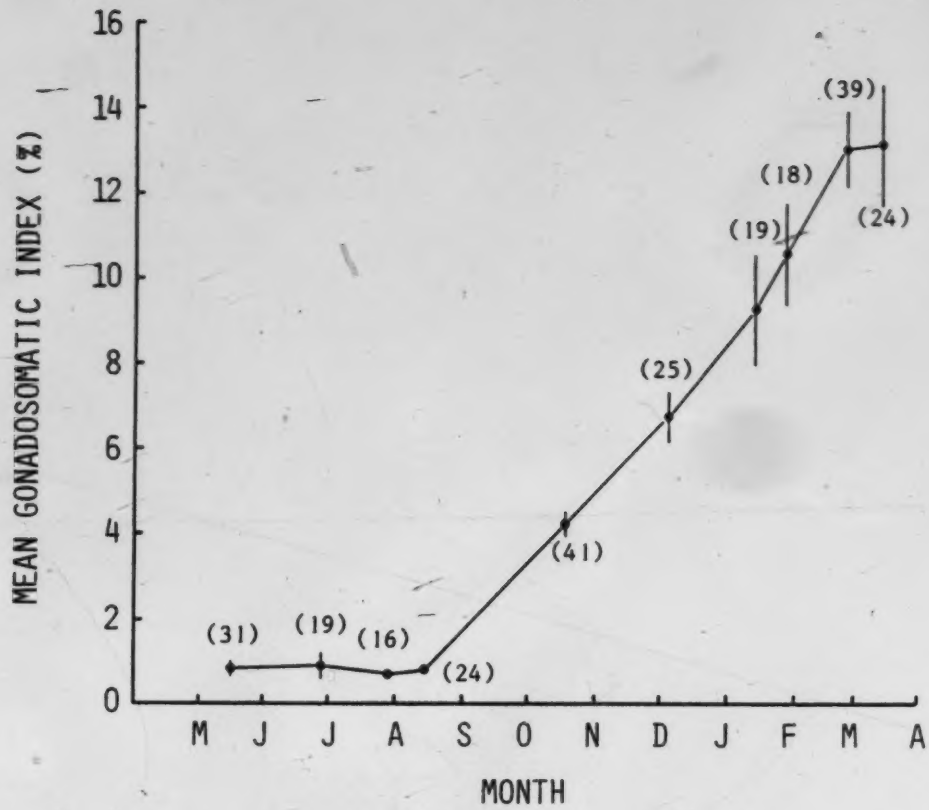

Fig. 3.14. Gonadosomatic index for female yellow perch collected from Mayatan Lake between 15 May 1983 and 16 March 1984. The mean values are given with the 95% confidence limits. The numbers in parentheses correspond to the sample size.

D. DISCUSSION

The present study on the yellow perch differed from Treasurer and Holliday's (1981) work on the Eurasian perch in documenting: 1) recruitment of oocytes in early summer instead of the fall; 2) three rather than four layers in the chorion; 3) presence of *both* yolk vesicles and yolk granules, which differed in time of appearance, staining reaction, and location within the ooplasm; and 4) presence of preovulatory atresia of developing oocytes at Stages V and VI.

The histological observations reported here demonstrated that oocyte development in the yellow perch is a continuous, group-synchronous process. At all developmental stages of the ovary, two populations of oocytes - developing and resting - could be distinguished. Initially, only one size range (Fig. 3.1) of oocytes could be found in maturing virgins (Stage IID) and recovering spent (Stage IIR) females (Fig. 3.2). This was the situation in late May, immediately after spawning, when the GSI was lowest (Fig. 3.14). This set of oocytes, in various stages of primary growth preceding exogenous vitellogenesis, represents the population from which developing oocytes are recruited. In Stage IIR ovaries, two generations of oocytes probably exist: the resting oocytes from the previous year and new oocytes just formed from oogonia. This has been suggested by Aravindan and Padmanabhan (1972) for *Tilapia mossambica*. Which of these two superimposed generations of oocytes will be recruited for the current year is uncertain. However, there are indications that only the one-year old oocytes will undergo further development in the rainbow trout, *Salmo gairdneri* (Sumpter, personal communication), Pacific herring, *Clupea harengus* (Bowers and Holliday 1961), and three species of groupers from the genus *Epinephales* (Bouian and Siau 1983). Oocytes formed in the current year in groupers undergo detectable previtellogenic cytoplasmic pH changes that fail to show in oocytes from the previous year (Bouain and Siau 1983). Whether the smaller primary oocytes in Stage IIR (Fig. 3.2) correspond to the just recruited oocytes, and the larger primary oocytes, showing advanced nucleolar fragmentation and peripheral migration, to those from the previous year cannot be established on the basis of the present study. According to Macer (1974) recruitment and subsequent yolk vesicle formation in the horse

mackerel could be anticipated by the appearance of vacuolation in the cytoplasm. This corresponds to the stage just before endogenous vitellogenesis. The oocytes observed in the more advanced Stage IIR ovaries in this study (Fig. 3.3) appear to fit the description of this vacuolation stage.

The bimodal distribution in the size of oocytes of Stage III ovaries in late June (Fig. 3.4) signaled the histological differentiation of developing from resting oocytes. This dichotomy in developing and resting oocytes commenced during Stage III and persisted in subsequent stages. It should be noted that recruitment occurred without any change in the GSI (mean = 0.9%). The appearance of vitellogenic oocytes in late June in this study was earlier than documented in the Eurasian perch by Treasurer and Holliday (1981), who observed this same phenomenon in early September. In contrast to this study, the recruitment in September was accompanied by almost a doubling of the GSI. The time course of ovarian development of the population being studied may be different from that of the population studied by Treasurer and Holliday (1981). This may be related to adaptation of the reproductive cycle of the yellow perch near the northern edge of their distribution like the Alberta lakes where the onset of winter is earlier than in lakes from more southerly regions. This may also reflect a true species differences in reproductive cycles.

The majority of the resting oocytes were in the late primary growth phase (perinucleolar stage) and this stage persisted in all the samples throughout the year. These observations suggest that recruitment occurs precisely at the end of the gonadotropin-independent growth phase (Wallace and Selman 1981). As expected of teleosts showing this strategy of recruitment, a population of oocytes in the primary growth phase is present in the ovary throughout the year. From this population oocytes are recruited and these sequentially undergo vitellogenesis and maturation (Wallace and Selman 1981).

Data in Chapter 2 suggested that the yellow perch recruit a maximal number of oocytes into its developing stock early in oogenesis and this number was modulated downward by preovulatory oocyte degeneration. Factors that trigger preovulatory degeneration are unclear although they may be related to reduction in food supply (Scott 1962) or adverse

environmental factors (Kukaradze 1968; Kipling 1976). The occurrence of recruitment in early summer (late June) shows that the phenomenon precedes peak feeding activity in mid-summer (Schneider 1973; Thorpe 1977c) suggesting that the number of oocytes initially recruited is not dependent on the diversion of energy from the soma to the gonads. Hence, the initial number of oocytes recruited into the developing pool may somehow be genetically determined.

The appearance of basophilic yolk vesicles in Stage III oocytes agreed with previous observations on many other species cited by Wallace and Selman 1981. The yolk vesicles, sometimes termed intravesicular yolk (Marza et al. 1937), have been found to contain glycoprotein portions (Heesen and Engels 1973). The yolk vesicles eventually form the cortical alveoli which appear on the inner aspect of cytoplasmic membrane in subsequent stages of oocyte differentiation in herring, *Clupea pallasi* (Yamamoto 1956a), smelt, *Hypomesus japonicus* (Yamamoto 1956b), and zebrafish, *Brachydanio rerio* (Malone and Hisaoka 1963).

The emergence of developing oocytes in Stage III was paralleled by the appearance of granulosa cells (Fig. 3.5), which are believed to permit the acquisition of yolk and formation of chorion (Wallace and Selman 1981). The latter structure showed two distinct layers at this stage, an inner zona radiata and an outer tunica propria.

Late developing (Stage IV) (Fig. 3.6) oocytes occurred mostly in December when the GSI had increased to a mean of 6.7% which represents a 7.4-fold increase from an initial GSI of 0.9% in May. This increment in GSI was also accompanied by a clear size separation between larger developing and smaller resting oocytes (Fig. 3.11). The overlap in the size of the two types of oocytes before August could lead to an overestimation of fecundity if egg counts were done before this time. The increase in size of the developing oocytes, from a mean of 162 μm in May to a mean of 832 μm at this stage, was primarily due to the elaboration and accumulation of yolk granules in the center of the cytoplasm.

The most diagnostic feature of oocytes at this stage was the peripheral displacement of the yolk vesicles by the deposition of yolk granules. However, the report of Treasurer and Holliday (1981) on the Eurasian perch did not make any distinction between the yolk vesicles

and the yolk granules. It is highly possible that their use of Bouin's fixative, and hematoxylin and eosin stains did not allow them to detect subtle differences between these distinct structures. The yolk vesicles, correctly termed as cortical alveoli at this point (Wallace and Selman 1981), lined the inner margin of the oolemma. The cortical alveoli fuse with the oolemma and extrude their contents into the perivitelline space during cortical reaction at fertilization. Since the formation of the yolk vesicles and yolk granules overlapped, it was impossible to determine their relative contribution to the increase in cytoplasmic volume. In the teleosts, the yolk granules are formed by the transfer of phosphoprotein from the blood (Heesen and Engels 1973) via pinocytosis (Droller and Roth 1966; Gupta and Yamamoto 1972; Shackley and King 1977). Later stages revealed that these yolk granules, also called yolk spheres or yolk globules, maintained their integrity throughout oocyte growth giving rise to translucent eggs in the perch. In other species, the yolk granules coalesce centripetally eventually forming a homogenous mass of fluid yolk. This process makes some fish eggs very transparent (Wallace and Selman 1981).

The chorion at this and subsequent stages showed three distinct layers - an inner zona radiata, a wide middle layer, and an outer tunica propria (Fig. 3.9). Mansueti (1964) described the yellow perch chorion, which she termed as elastic egg case, as having three layers, an inner zona radiata, a middle radially-striated elastic layer, and an outer adhesive layer. The middle layer undoubtedly corresponds to the middle chorionic layer observed in this study. Treasurer and Holliday (1981) observed in late Stage IV oocytes of Eurasian perch two lamellae within the middle layer, giving a total of four chorionic layers. Their observation was not corroborated in this study. This discrepancy could be related to their use of the highly acidic Bouin's fixative which is known to destroy some cell organelles (Bloom and Fawcett 1968). Hence, the additional lamellae seen in the Eurasian perch oocyte could just be an artifact since it was not seen in the present study which used a gentler and buffered fixative.

There is considerable controversy surrounding the measurements and numbers of layers in the chorion (Lonning 1972). Some of the controversy concerning thickness and numbers of chorionic elements may be attributed to differences in histological preparations

and limitations of light microscopy. Moreover, variations in the usage of terms may also contribute to the confusion (Kuchnow and Scott 1977). For example, the chorion had been called elastic middle layer (Ryder 1887), elastic egg case (Mansueti 1964), plasma membrane (Sterba 1957), and jelly coat (Gotting 1965).

Gravid ovaries (Stage V), representative of samples in February, showed developing oocytes that had attained a mean diameter of 1,004 μm, a six-fold increase from an initial mean diameter of 162 μm in May. This increase in size could be traced to further yolk granule deposition and thickening of the middle chorion (Fig. 3.7). The GSI (mean = 13.0%) reflected also the growth in oocytes. The preponderance of circular structures among the yolk granules could possibly be sites of lipid accumulation. Lipid globules are prominent in fresh perch eggs (Mansueti 1964) and previous observations indicate that lipid deposition in perch eggs commences in November during the early Stage IV (Le Cren 1951; Koshelev 1963). The yolk granules, previously non-staining, were now basophilic suggesting a possible pH shift in their contents as part of the maturation process. Oocytes in spawning ovaries (Stage VI) showed further growth primarily due to the thickening of the middle chorion (Fig. 3.8). In many fish eggs, the increase in oocyte diameter during maturation is due to hydration as corroborated by *in vivo* observations on carp, goldfish (Clemens and Grant 1964), ayu (Hirose and Ishida 1974), and Japanese flounder (Hirose et al. 1976) eggs, and by *in vitro* observations on medaka, ayu (Hirose 1976), killifish (Wallace and Selman 1978), and sticklebacks (Wallace and Selman 1979). About 77% of the final egg volume is formed during spawning in the cunner, *Tautogolabrus adspersus* (Wallace and Selman 1981).

Preovulatory oocyte degeneration was observed in Stages V and VI ovaries. This could possibly explain the progressive decline in fecundity of the yellow perch with the approach of the spawning season (see Chapter 2). Atresia has been found to be common in some lake populations of the Eurasian perch in New Zealand (Graynoth, per. comm., cited by Jellyman 1980). However, Treasurer and Holliday (1981) reported no atresia in the same species. Preovulatory atresia may be very extensive; it reduced the number of eggs spawned in sturgeon (Badenko et al. 1973) and haddock (Robb 1982). Mass degeneration of oocytes has

been reported in many species including creek chubsucker (Wagner and Cooper 1963), pike-perch (Kukaradze 1968), brook trout (Wydoski and Cooper 1966), horse mackerel (Macer 1974), dace (Wilkinson and Jones 1977), and Greenland halibut (Walsh and Bowering 1982). Food supply (Scott 1962; Macer 1974; Robb 1982) and adverse environmental factors (Sakun 1957; Kukaradze 1968; Kipling 1976) have been implicated in precipitating resorption of maturing eggs.

The time course of the increase in the diameter and volume of developing oocytes has not been investigated in both the yellow and Eurasian perch. The present study showed that the growth in size of the oocyte has two components: 1) increase in ooplasmic volume from Stage IID to III primarly through the accumulation of yolk granules from summer to fall, and 2) increase in the thickness of the chorion, particularly the middle layer, from Stage III to VI over the winter months. At Stage VI almost 70% of the total mean oocyte volume was contributed by the chorion. Upon fertilization, the yellow perch egg is capable of increasing its diameter twofold via the uptake of water by the chorion (Mansueti 1964). The significance of the diversion of presumably large amount of energy to chorion thickening is still unclear but it could be an adaptation to demersal mode of dispersion of the eggs. Mansueti (1964) suggested that the thick chorion provides protection not only from abrasion and bumping, but also from predators since it is extremely difficult to pierce the chorion once it has hardened due to the uptakeof water. Moreover, the incubation period of the fertilized perch egg is significantly longer than most temperate freshwater fish that a thick chorion is of survival value.

E. CONCLUSIONS AND SUMMARY

(1) The histology of the different stages of oocyte maturation described in this study for the yellow perch agrees well with the descriptions given for the Eurasian perch by Treasurer and Holliday (1981). However, the subdivision of the middle chorion into two distinct layers was not corroborated in the present study. This study also documented the presence of both yolk vesicles and yolk granules, which were not demonstrated in the Eurasian

perch. These differences may be attributed to differences in fixatives and stains used to prepare the histological sections of the ovaries.

(2) Recruitment, as evidenced by histology and by the bimodal distribution of resting and developing oocytes, occurred at Stage III (developing early) in June. The time of recruitment occurred before peak feeding activity, which does not happen until midsummer. This indicated that recruitment was not dependent on the diversion of stored energy from the soma to the gonads. No increase in the GSI was observed at the time of recruitment.

(3) The increase in size of the developing oocytes from Stages IID to III was due to the increase in ooplasmic volume. The thickening of the middle chorionic layer could account for the increased size of the oocytes from Stages IV to VI.

(4) During the course of ovarian recrudescence from mid May to mid March of the following year, the developing oocytes increased 6.2 times in diameter and 239.5 times in volume. The GSI increased increased 15.4-fold over the same period of time.9

(5) Preovulatory resorption of oocytes was observed in half of the sections of Stages V and VI ovaries examined. No previous report of preovulatory atresia in the yellow perch is known.

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IV. CONCLUDING DISCUSSION

The present paper provides evidence that counting developing oocytes before late Stage IV (Kesteven 1960) in the yellow perch leads to an overestimation of the actual fecundity. In the perch I examined there was a gradual decline in the fecundity with the approach of the spawning season. This finding supports the theory of Hislop et al. (1978) and Robb (1982) that the upper limit of fecundity in the fish is determined early in oogenesis, and this maximum number is modulated downward by adverse environmental factors. Blaxter and Holliday (1963) suggested that the upper ceiling of potential fecundity of a fish is genetically determined. However, maximum potential fecundity is realized only when proximal factors, such as water temperature and food availability, are optimal.

The finding that fecundity decreases over time in yellow perch is significant in two ways. First, it points to the need for a critical reevaluation of previously published reports on the fecundity of both yellow and Eurasian perch which used females sampled at various times before spawning. The assumption, that once oocytes are recruited into the developing stock their number does not change significantly over time, underlies the practice of 1) determining fecundity many months before spawning (Sheri and Power 1969); 2) comparing fecundities of samples collected at different times of the year (Tsai and Gibson 1971); and 3) calculating fecundity for a pooled sample of females collected over a period of months before spawning (Mann 1978). The validity of this assumption and the practices it had spawned are certainly put into question by the finding mentioned above.

Second, this finding reveals a heretofore undocumented degree of plasticity in the fecundity of the yellow perch. According to Mann and Mills (1979), it is common for fish living in harsh unstable environments to modify their reproductive tactics to ensure the survival of the young. Hence, it is not surprising that the perch populations studied modify their reproductive strategy since they are found in lakes that are close to the northern limit of the species geographic range where the promixal factors are extreme. By reducing the number of developing oocytes at a time when the population is presumably food limited, yellow perch opt for a trade-off between egg number and egg size, i.e., the species ensure the continued

growth of fewer oocytes but larger oocytes. The same strategy is also employed by the herring, *Clupea harengus* (Hempel and Blaxter 1967). This strategy is effective because fry survival is directly proportional to the size of the egg (Bagenal 1969). Other strategies employed by fish found near or at the edge of their respective ranges include variation in the number of batches of eggs produced in one spawning season, e.g., bullhead, *Cottus gobio* (Fox 1978), and production of eggs with a very wide range of sizes, e.g., dace, *Leuciscus leuciscus* (Mann and Mills 1979).

The second major finding of the present work is the inverse relationship between growth rates of perch from different populations and fecundity. If a temporal decline in fecundity during recrudescence is a short-term response to fluctuations in the environment, the inverse relationship between growth rate and fecundity represents a long-term response to local conditions. Preliminary data show that the stunted slow-growing perch populations from Narrow Lake and Lac Ste. Anne have shorter lifespan than the fast-growing populations from Mayatan Lake and Thunder Lake. If this is true, then there is also an inverse relationship between fecundity and lifespan in the populations studied. This then is consistent with the commonly observed trade-off between reproductive effort and longevity (Mann and Mills 1979). The long-lived perch appear to spread out their reproductive effort over their longer lifespan than the short-lived perch. This phenomenon has also been documented in chub, *Leuciscus cephalus* (Mann 1976) and dace, *Leuciscus leuciscus* (Mann 1974).

Histological examination of the ovary during recrudescence demonstrated evidence of preovulatory atresia in Stages V and VI (Kesteven 1960) ovaries. This could account for the observed temporal decline in the fecundity of the yellow perch during recrudescence. The study of the size distribution of resting and developing oocytes, and the time course of the growth of the developing oocytes provided some insights into the artifacts that could be introduced into the methods of determing fecundity in the fish. Detailed histological descriptions of the ovarian cycle in the yellow perch also showed some significant differences with the histological description of the ovary of the Eurasian perch as previously reported by Treasurer and Holliday (1981). The better resolution of cytological structures in the present

study suggests that glutaraldehyde fixation and plastic embedding are more advantageous than the use of acidic fixatives and paraffin for embedding.

In summary, the present work has attempted to document through study of fecundity and ovarian recrudescence both shortand long-term modifications in the reproductive stategy of the yellow perch found in habitats that are near the northern limits of its distribution. It is hypothesized that the observed trade-offs between egg number and egg size, and between egg number and lifespan represent adaptations to the latitudinal and local characteristics of the habitat of the fish.

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Appendix I. Table 1. Time of sampling and documented time of spawning of yellow perch and Eurasian perch used in fecundity studies.

Investigator(s)	Study Area	Latitude	Time of Sampling for Fecundity Estimation	Reported Spawning at Locality or Latitude
Perca flavescens				
Pearse (1925)	Lake Mendota	43° N	20-21 April 1921	April (Hergenrader 1969)
Muncy (1962)	Severn River (Maryland)	39° N	March 1961	March (Muncy 1962)
Sheri & Power (1969)	Lake Ontario	44° N	Summer 1967	May-June (Sheri & Power 1969)
Tsai & Gibson (1971)	Patuxent River (Maryland)	38° N	20-25 March 1969	March (Tsai & Gibson 1971)
Brazo et al. (1975)	Lake Michigan	42°-47° N	April-May 1974	April-May (Herman et al. 1964)
Perca fluviatilis				
Mann (1978)	River Stour (England)	51° N	January-May 1974	April-May (Craig 1974)
Jellyman (1980)	Lake Pounnui (New Zealand)	41° S	July-December 1975	September*
Bregazzi & Kennedy (1982)	Slapton Ley (England)	50° N	October 1974-June 1977	April-May (Craig 1974)

*Expected time of spawning

Appendix 1. Table 2. Comparison of variability of ten triplicate weighings of dried oocytes to test the reliability of the procedure for determining fecundity. All the oocytes were taken from one fish.

	Groups									
	1	2	3	4	5	6	7	8	9	10
Weights of 200 oocytes (g)										
(a)	0.1983	0.1969	0.1970	0.1971	0.1959	0.1972	0.1978	0.2035	0.1969	0.1965
(b)	0.1977	0.1870	0.1986	0.1985	0.1861	0.1979	0.1969	0.1959	0.1984	0.1999
(c)	0.1901	0.1934	0.1986	0.1980	0.1980	0.1982	0.1989	0.1992	0.1971	0.1970
Mean weight of 200 oocytes (g)	0.1954	0.1924	0.1980	0.1979	0.1933	0.1978	0.1979	0.1995	0.1975	0.1978
Fecundity estimated from mean weight of 200 oocytes	9,576	9,724	9,450	9,455	9,680	9,459	9,455	9,379	9,474	9,459
Difference from mean fecundity estimate	65	213	-61	-56	169	-52	-56	-132	-37	-52
Difference as % of mean fecundity estimate	0.68%	2.24%	-0.64%	-0.59%	1.78%	-0.55%	-0.59%	-1.39%	-0.30%	-0.55%

Total weight of dried oocytes: 9.3554 grams. Mean fecundity estimate ± 95% confidence limits: 9,511 ± 70

Appendix 1. Table 3. Relationship between total length (cm) and fecundity of yellow perch, collected from Mayatan Lake, Alberta, expressed as $\log_{10}$ fecundity = $\log_{10}$ a + b ($\log_{10}$ total length).

Sampling Date	Number of Females	a ± 95% Confidence Limits	b[1] ± 95% Confidence Limits	Correlation Coefficient[2]
1983				
8 October	34	-1.685 ± 0.965	4.354 ± 0.756	0.90
5 December	24	-1.331 ± 0.437	4.064 ± 1.426	0.78
1984				
14, 28 January	34	-0.904 ± 0.214	3.681 ± 0.617	0.91
27 February	32	-0.698 ± 0.297	3.509 ± 0.830	0.84
15 March	23	-1.001 ± 0.406	3.743 ± 1.207	0.82

[1]The slopes were not significantly different from each other at $P < 0.05$. The equality of slopes was tested using analysis of covariance.

[2]F statistics for the correlation coefficients (r) were all significant at $P < 0.001$.

Appendix 1. Table 4. Comparisons of slopes and elevations of log_{10} *fecundity* on log_{10} *total length* of yellow perch collected from Mayatan Lake, Alberta, between 8 October 1983 and 15 March 1984.[1]

Regression Lines Compared	Equality of Slopes		Equality of Elevations	
	F	P	F	P
A, B, C, D, and E[2]	0.680	0.61	5.550	<0.001
A and B	0.145	0.70	0.103	0.75
A, C, D, and E	0.893	0.45	6.412	<0.001
A and C	1.987	0.16	11.766	<0.01
A, D, and E	1.075	0.35	7.415	<0.01
A and D	2.241	0.14	10.771	<0.01
A and E	0.863	0.36	8.853	<0.01
B, C, D, and E	0.158	0.92	2.359	0.08

[1]Analysis of covariance was used to test the equality of slopes and elevations of the regression lines at a significance level of 0.05.

Ho: there were no significant differences in the slopes (or elevations) of the regressions of log_{10} *fecundity* on log_{10} *total length* of samples collected on two or more different sampling dates.

[2]A refers to the regression for samples collected on 8 October 1983; B, 5 December 1983; C, 14 & 28 January 1984; D, 27 February 1984; and E, 15 March 1984.

Appendix 1. Table 5. Comparisons of total lengths of female yellow perch of the same age from Mayatan Lake, Alberta, using one-way anova.[1]

Age	Sampling Date	Number of Females	Mean Total Length (cm) ± 95% Confidence Limit	F
III+	8 October 1983	2	15.5 ± 6.35	0.31[ns][2]
	14, 28 January 1984	9	15.2 ± 0.49	
	15 March 1984	4	15.1 ± 0.55	
IV+	8 October 1983	5	16.3 ± 1.18	0.25[ns]
	14, 28 January 1984	8	16.8 ± 0.99	
	15 March 1984	8	16.6 ± 1.06	
V+	8 October 1983	7	17.7 ± 0.67	1.83[ns]
	14, 28 January 1984	15	18.8 ± 0.89	
	15 March 1984	10	18.4 ± 0.50	
VI+	8 October 1983	14	19.5 ± 0.59	0.91[ns]
	14, 28 January 1984	7	20.3 ± 1.71	
	15 March 1984	2	20.2 ± 1.46	

[1] *Ho:* There was no significant difference in the mean total lengths of female fish of the same age collected at different dates.

[2] ns - not significant at $P < 0.05$

Appendix 1. Table 6. Relationship between total length (cm) and fecundity of yellow perch, collected from four Alberta lakes, expressed as $\log_{10}$ *fecundity* = $\log_{10}$ a + b ($\log_{10}$ *total length*).

Lake	Number of Females	a ± 95% Confidence Limits	b[1] ± 95% Confidence Limits	Correlation Coefficient[2]
Mayatan[3]	89	-0.917 ± 0.548	3.685 ± 0.437	0.87
Ste. Anne[4]	90	-0.252 ± 0.294	3.360 ± 0.240	0.95
Thunder[5]	30	-0.901 ± 0.052	3.822 ± 0.823	0.87
Narrow[6]	9	-0.342 ± 0.208	3.584 ± 0.640	0.98

[1]The slopes were not significantly different from each other at $P > 0.05$. The equality of slopes was tested using analysis of covariance.

[2]F statistics for the correlation coefficients (r) were all significant at $P < 0.001$.

[3]Samples were collected between 14 January and 15 March 1984. The samples were pooled because of equality of slopes and elevations of $\log_{10}$ *fecundity* on $\log_{10}$ *total length* regressions at $P < 0.05$.

[4]Samples were collected on 23 February 1983 and 17 February 1984. The samples were pooled because of equality of slopes and elevations of $\log_{10}$ *fecundity* on $\log_{10}$ *total length* regressions at $P < 0.05$.

[5]Sample was collected on 22 February 1984.

[6]Sample was collected on 23 February 1984.

Appendix 1. Table 7. Comparisons of slopes and elevations of log_{10} *fecundity* on log_{10} *total length* regressions of yellow perch collected from four Alberta lakes on February 1984.[1]

Regression Lines Compared	Equality of Slopes		Equality of Elevations	
	F	P	F	P
NL, LSA, TL, and ML[2]	0.804	0.49	195.638	<0.001
NL and ML	0.047	0.83	127.486	<0.001
NL, LSA, and TL	0.844	0.43	31.568	<0.001
NL and TL	0.234	0.63	36.573	<0.001
NL and LSA	0.536	0.47	46.303	<0.001
LSA, TL, and ML	0.059	0.81	108.116	<0.001
LSA and ML	1.796	0.18	450.426	<0.001
LSA and TL	1.344	0.25	18.433	<0.001
TL and ML	0.059	0.81	108.116	<0.001

[1]Analysis of variance was used to test the equality of slopes and elevations of regression lines at a significance level of 0.05.

Ho: there was no significant difference in the slopes (or elevations) of the regressions of log_{10} *fecundity* on log_{10} *total length* of samples collected from two or more different lakes.

[2]NL refers to the regression for samples collected from Narrow Lake; LSA, from Lac Ste. Anne; TL, from Thunder Lake; and ML, from Mayatan Lake.

Appendix I. Table 8. Relationship between somatic weight (gm) and fecundity of yellow perch, collected from four Alberta lakes, expressed as $fecundity = a + b\ (somatic\ weight)$.[1]

Lake	Number of Females	a ± 95% Confidence Limits	b ± 95% Confidence Limits	Correlation Coefficient[2]
Mayatan[3]	32	-1,334.86 ± 272.27	140.07 ± 26.82	0.89
Ste. Anne[4]	36	-263.62 ± 301.11	162.44 ± 17.92	0.95
Thunder[5]	30	-3,068.61 ± 460.69	205.89 ± 35.87	0.91
Narrow[6]	9	-1,006.58 ± 657.97	306.29 ± 72.09	0.97

[1]The slopes and elevations of the regression lines could not be compared because of heterogenous residual variances.

[2]F statistics for the correlation coefficients (r) were all significant at $P < 0.001$.

[3]Sample was collected on 27 February 1984.

[4]Sample was collected on 17 February 1984.

[5]Sample was collected on 22 February 1984.

[6]Sample was collected on 23 February 1984.

Appendix 1. Table 9. Relationship between ovary weight (gm) and fecundity of yellow perch, collected from four Alberta lakes, expressed as $fecundity = a + b\ (ovary\ weight)$.[1]

Lake	Number of Females	a ± 95% Confidence Limits	b ± 95% Confidence Limits	Correlation Coefficient[2]
Mayatan[3]	32	481.57 ± 301.71	729.94 ± 159.93	0.86
Ste. Anne[4]	36	1,118.96 ± 958.44	804.66 ± 89.74	0.96
Thunder[5]	30	-295.57 ± 191.84	1,140.58 ± 76.59	0.98
Narrow[6]	9	-204.86 ± 224.03	1,225.97 ± 95.37	0.99

[1]The slopes and elevations of the regression lines could not be compared because of heterogenous residual variances.

[2]F statistics for the correlation coefficients (r) were all significant at $P < 0.001$.

[3]Samples was collected on 27 February 1984.

[4]Sample was collected on 17 February 1984.

[5]Sample was collected on 22 February 1984.

[6]Sample was collected on 23 February 1984.

Appendix 1. Table 10. Relationship between age (years) and fecundity of yellow perch, collected from three Alberta lakes, expressed as $\log_{10}$ fecundity = $\log_{10} a + b$ ($\log_{10}$ age).[1]

Lake	Number of Females	a ± 95% Confidence Limits	b ± 95% Confidence Limits	Correlation Coefficient[2]
Mayatan[3]	32	2.750 ± 0.219	1.433 ± 0.480	0.74
Ste. Anne[4]	36	2.764 ± 0.132	1.610 ± 0.336	0.86
Narrow[5]	9	2.642 ± 0.223	1.685 ± 0.576	0.93

[1]The slopes and elevations of the regression lines could not be compared because of heterogenous residual variances.

[2]F statistics for the correlation coefficients (r) were all significant at $P < 0.001$.

[3]Sample was collected on 27 February 1984.

[4]Sample was collected on 17 February 1984.

[5]Sample was collected on 23 February 1984.

Appendix 1. Table 11. Fecundity of the various age groups of yellow perch collected from four Alberta lakes.

Lake	Age Group	Number of Females	Fecundity Range	Fecundity Mean		95% C.L.[1]
Mayatan[2]	III+	6	2,346 - 3,979	3,242	±	650
	IV+	32	1,909 - 6,583	3,837	±	366
	V+	36	2,420 -13,233	6,535	±	772
	VI+	12	4,454 -11,057	7,516	±	1,253
	VII+	3	7,227 -13,188	9,395	±	8,189
Ste. Anne[3]	III+	12	2,487 - 5,177	3,617	±	606
	IV+	19	3,995 - 7,117	5,300	±	385
	V+	38	4,660 -19,000	7,831	±	688
	VI+	19	7,593 -15,042	10,862	±	1,009
	VII+	2	11,175 -19,000	15,088	-	-
Thunder[4]	III+	10	7,562 - 8,045	7,552	±	1,229
	IV+	36	4,997 -13,416	9,501	±	805
	V+	14	5,258 -15,460	11,327	±	1,744
	VI+	4	4,179 -18,292	14,128	±	6,906
Narrow[5]	II+	1	-	1,747	-	-
	III+	3	2,276 - 2,678	2,477	-	-
	IV+	1	-	3,295	-	-
	V+	4	5,560 -10,124	7,406	±	3,136
	VI+	1	-	8,935	-	-

[1] C.L. = confidence limits

[2] Samples were collected between 14 January and 15 March 1984.

[3] Samples were collected between 23 February 1983 and 12 March 1984.

[4] Samples were collected in 22 February and 16 March 1984.

[5] Sample was collected in 23 February 1984.

Appendix 1. Table 12. Correlation coefficients (r) between logarithmically transformed variables for yellow perch from four Alberta lakes.

Lake	Variable	Total Length	Somatic Weight	Ovary Weight	Fecundity
Mayatan[1]	Total Length				0.84
	Somatic Weight	0.91			0.89
	Ovary Weight	0.72	0.85		0.86
	Age	0.79	0.80	0.68	0.79
Ste. Anne[2]	Total Length				0.91
	Somatic Weight	0.95			0.91
	Ovary Weight	0.91	0.96		0.96
	Age	0.92	0.89	0.86	0.84
Thunder[3]	Total Length				0.87
	Somatic Weight	0.95			0.91
	Ovary Weight	0.86	0.90		0.98
	Age	0.49	0.54	0.57	0.52
Narrow[4]	Total Length				0.97
	Somatic Weight	0.99			0.97
	Ovary Weight	0.97	0.97		0.99
	Age	0.95	0.92	0.91	0.89

[1]Sample was collected on 27 February 1984. Sample size was 32.

[2]Sample was collected on 17 February 1984. Sample size was 36.

[3]Sample was collected on 22 February 1984. Sample size was 30.

[4]Sample was collected on 23 February 1984. Sample size was 9.

Appendix 1. Table 13. Four-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ ovary weight (X_1), $\log_{10}$ age (X_2), $\log_{10}$ total length (X_3), and $\log_{10}$ somatic weight (X_4) for yellow perch collected from Mayatan Lake on 27 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	4	0.545808	0.136452	41.44	<0.001
Test of b_1 (ovary weight)	1	0.028748	0.028748	8.73	<0.001
Test of b_2 (age)	1	0.006718	0.006718	2.04	n.s.[2]
Test of b_3 (total length)	1	0.002470	0.002470	0.75	n.s.
Test of b_4 (somatic weight)	1	0.000922	0.000922	0.28	n.s.
Error	27	0.088922	0.003293		
Total	31	0.634730			

[1]Mutiple regression equation: $\log_{10} Y = 1.8011 + 0.5124 \log_{10} X_1 + 0.3151 \log_{10} X_2 + 0.7533 \log_{10} X_3 + 0.2059 \log_{10} X_4$

Multiple correlation coefficient: r = 0.93

[2]n.s. - not significant

Appendix 1. Table 14. Four-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ ovary weight (X_1), $\log_{10}$ total length (X_2), $\log_{10}$ age (X_3), and $\log_{10}$ somatic weight (X_4) for yellow perch collected from Lac Ste. Anne on 17 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square		
All slopes (b_i)	4	1.159260	0.289815	94.75	<0.001
Test of b_1 (ovary weight)	1	0.025114	0.025114	8.21	<0.01
Test of b_2 (total length)	1	0.008382	0.008382	2.74	n.s.[2]
Test of b_3 (age)	1	0.005017	0.005017	1.64	n.s.
Test of b_4 (somatic weight)	1	0.003334	0.003334	1.09	n.s.
Error	31	0.094823	0.003059		
Total	35	1.254083			

[1]Multiple regression equation: $\log_{10} Y = 1.5254 + 0.4225 \log_{10} X_1 + 1.4048 \log_{10} X_2 + 0.3084 \log_{10} X_3 + 0.2760 \log_{10} X_4$

Multiple correlation coefficient: r = 0.95

[2]n.s. - not significant

Appendix 1. Table 15. Four-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ ovary weight (X_1), $\log_{10}$ age (X_2), $\log_{10}$ somatic weight (X_3), and $\log_{10}$ total length (X_4) for yellow perch collected from Thunder Lake on 22 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	4	0.488229	0.122057	162.58	<0.001
Test of b_1 (ovary weight)	1	0.066486	0.066486	88.53	<0.001
Test of b_2 (age)	1	0.004611	0.004611	6.14	<0.025
Test of b_3 (somatic weight)	1	0.000571	0.000571	0.76	n.s.[2]
Test of b_4 (total length)	1	0.000195	0.000195	0.26	n.s.
Error	25	0.018769	0.000751		
Total	29	0.506998			

[1]Multiple regression equation: $\log_{10} Y = 2.5657 + 0.9342 \log_{10} X_1 - 0.2180 \log_{10} X_2 + 0.1821 \log_{10} X_3 + 0.2715 \log_{10} X_4$

Multiple correlation coefficient: r = 0.98

[2]n.s. - not significant

Appendix 1. Table 16. Three-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ ovary weight (X_1), $\log_{10}$ age (X_2), and $\log_{10}$ somatic weight (X_3) for yellow perch collected from Narrow Lake on 23 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	3	0.618839	0.206280	1,090.21	<0.001
Test of b_1 (ovary weight)	1	0.232050	0.232050	122.78	<0.001
Test of b_2 (age)	1	0.000359	0.000359	1.90	n.s.[2]
Test of b_3 (somatic weight)	1	0.000289	0.000289	1.53	n.s.
Error	5	0.000946	0.000189		
Total	9	0.619785			

[1]Mutliple regression equation: $\log_{10} Y = 2.9724 + 0.9843 \log_{10} X_1 - 0.1413 \log_{10} X_2 + 0.1492 \log_{10} X_3$

Multiple correlation coefficient: r = 1.00

[2]n.s. - not significant

Appendix 1. Table 17. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ ovary weight (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Thunder Lake on 22 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	3	0.485068	0.242534	298.6	<0.001
Test of b_1 (ovary weight)	1	0.403239	0.403239	496.6	<0.001
Test of b_2 (age)	1	0.003873	0.003873	4.8	<0.05
Error	27	0.021931	0.000812		
Total	29	0.506999			

[1]Multiple regression equation: $\log_{10} Y = 3.0625 + 1.0920 \log_{10} X_1 - 0.1987 \log_{10} X_2$

Multiple correlation coefficient: r = 0.99

Appendix 1. Table 18. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ somatic weight (X_1) and $\log_{10}$ total length (X_2) for yellow perch collected from Mayatan Lake on 27 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	0.510700	0.255349	59.70	<0.001
Test of b_1 (somatic weight)	1	0.058039	0.058039	13.57	<0.001
Test of b_2 (total length)	1	0.000813	0.00813	0.19	n.s.[2]
Error	29	0.120431	0.427694		
Total	31	0.631010			

[1]Multiple regression equation: $\log_{10} Y = 1.3650 + 1.1042 \log_{10} X_1 + 0.3982 \log_{10} X_2$

Multiple correlation coefficient: r = 0.90

[2]n.s. - not significant

Appendix 1. Table 19. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ somatic weight (X_1) and $\log_{10}$ total length (X_2) for yellow perch collected from Lac Ste. Anne on 17 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	1.131714	0.565857	152.60	<0.001
Test of b_1 (somatic weight)	1	0.016760	0.016760	4.52	<0.05
Test of b_2 (total length)	1	0.012718	0.012718	3.43	n.s.[2]
Error	33	0.122367	0.003708		
Total	35	1.254061			

[1]Multiple regression equation: $\log_{10} Y = 0.9607 + 0.5443 \log_{10} X_1 + 1.6324 \log_{10} X_2$

Multiple correlation coefficient: r = 0.95

[2]n.s. - not significant

Appendix 1. Table 20. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ somatic weight (X_1) and log total length (X_2) for yellow perch collected from Thunder Lake on 17 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	0.420812	0.210406	65.92	<0.001
Test of b_1 (somatic weight)	1	0.033580	0.033580	10.52	<0.005
Test of b_2 (total length)	1	0.000606	0.000606	0.19	n.s.[2]
Error	27	0.086186	0.003192		
Total	29	0.506998			

[1]Multiple regression equation: $\log_{10} Y = 1.2530 + 1.1827 \log_{10} X_1 + 0.4754 \log_{10} X_2$

Multiple correlation coefficient: r = 0.91

[2]n.s. - not significant

Appendix 1. Table 21. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ total length (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Mayatan Lake on 27 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	0.466089	0.233045	40.08	<0.001
Test of b_1 (total length)	1	0.161126	0.161126	19.77	<0.001
Test of b_2 (age)	1	0.018827	0.018827	2.31	n.s.[2]
Error	29	0.168640	0.005815		
Total	31	0.634729			

[1]Multiple regression equation: $\log_{10} Y = -0.0698 + 2.7774 \log_{10} X_1 + 0.4398 \log_{10} X_2$

Multiple correlation coefficient: r = 0.86

[2]n.s. - not significant

Appendix 1. Table 22. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ total length (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Lac Ste. Anne on 17 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	1.115217	0.557609	132.51	<0.001
Test of b_1 (total length)	1	0.191506	0.191506	45.51	<0.001
Test of b_2 (age)	1	0.000295	0.000295	0.07	n.s.[2]
Error	33	0.138866	0.004208		
Total	35	1.254083			

[1]Multiple regression equation: $\log_{10} Y = -0.4652 + 3.5850 \log_{10} X_1 - 0.0701 \log_{10} X_2$

Multiple correlation coefficient: r = 0.94

[2]n.s. - not significant

Appendix 1. Table 23. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ total length (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Thunder Lake on 22 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	0.387279	0.193640	43.67	<0.001
Test of b_1 (total length)	1	0.305325	0.305325	68.86	<0.001
Test of b_2 (age)	1	0.000044	0.000044	0.01	n.s.[2]
Error	27	0.119719	0.004434		
Total	29				

[1]Multiple regression equation: $\log_{10} Y = -0.9134 + 3.8411 \log_{10} X_1 - 0.0181 \log_{10} X_2$

Multiple correlation coefficient: $r = 0.87$

[2]n.s. - not significant

Appendix 1. Table 24. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ total length (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Narrow Lake on 23 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	0.595932	0.297966	74.95	<0.001
Test of b_1 (total length)	1	0.055133	0.055133	13.87	<0.025
Test of b_2 (age)	1	0.000358	0.000358	0.09	n.s.[2]
Error	6	0.023852	0.003975		
Total	8	0.619784			

[1]Multiple regression equation: $\log_{10} Y = -0.1371 + 3.3276 \log_{10} X_1 + 0.1337 \log_{10} X_2$

Multiple correlation coefficient: r = 0.98

[2]n.s. - not significant

Appendix 1. Table 25. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ somatic weight (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Mayatan Lake on 27 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	0.517055	0.258527	63.71	<0.001
Test of b_1 (somatic weight)	1	0.165932	0.165932	40.89	<0.001
Test of b_2 (age)	1	0.007183	0.007183	1.77	n.s.[2]
Error	29	0.117675	0.117675		
Total	31	0.634730			

[1]Multiple regression equation: $\log_{10} Y = 1.7335 + 1.0601 \log_{10} X_1 + 0.3105 \log_{10} X_2$

Multiple correlation coefficient: r = 0.90

[2]n.s. - not significant

Appendix 1. Table 26. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ somatic weight (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Lac Ste. Anne on 17 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	1.119253	0.559627	136.97	<0.001
Test of b_1 (somatic weight)	1	0.185943	0.185943	45.51	<0.001
Test of b_2 (age)	1	0.000285	0.000285	0.07	n.s.[2]
Error	33	0.134830	0.004086		
Total	35	1.254083			

[1] Multiple regression equation: $\log_{10} Y = -0.4652 + 3.5850 \log_{10} X_1 - 0.0701 \log_{10} X_2$

Multiple correlation coefficient: $r = 0.94$

[2] n.s. - not significant

Appendix 1. Table 27. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ somatic weight (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Thunder Lake on 22 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	0.421098	0.210549	66.19	<0.001
Test of b_1 (somatic weight)	1	0.339095	0.339095	106.60	<0.001
Test of b_2 (age)	1	0.000891	0.000891	0.28	n.s.[2]
Error	27	0.085900	0.003181		
Total	29	0.506998			

[1]Multiple regression equation: $\log_{10} Y = 1.5872 + 1.3674 \log_{10} X_1 - 0.0949 \log_{10} X_2$

Multiple correlation coefficient: r = 0.91

[2]n.s. - not significant

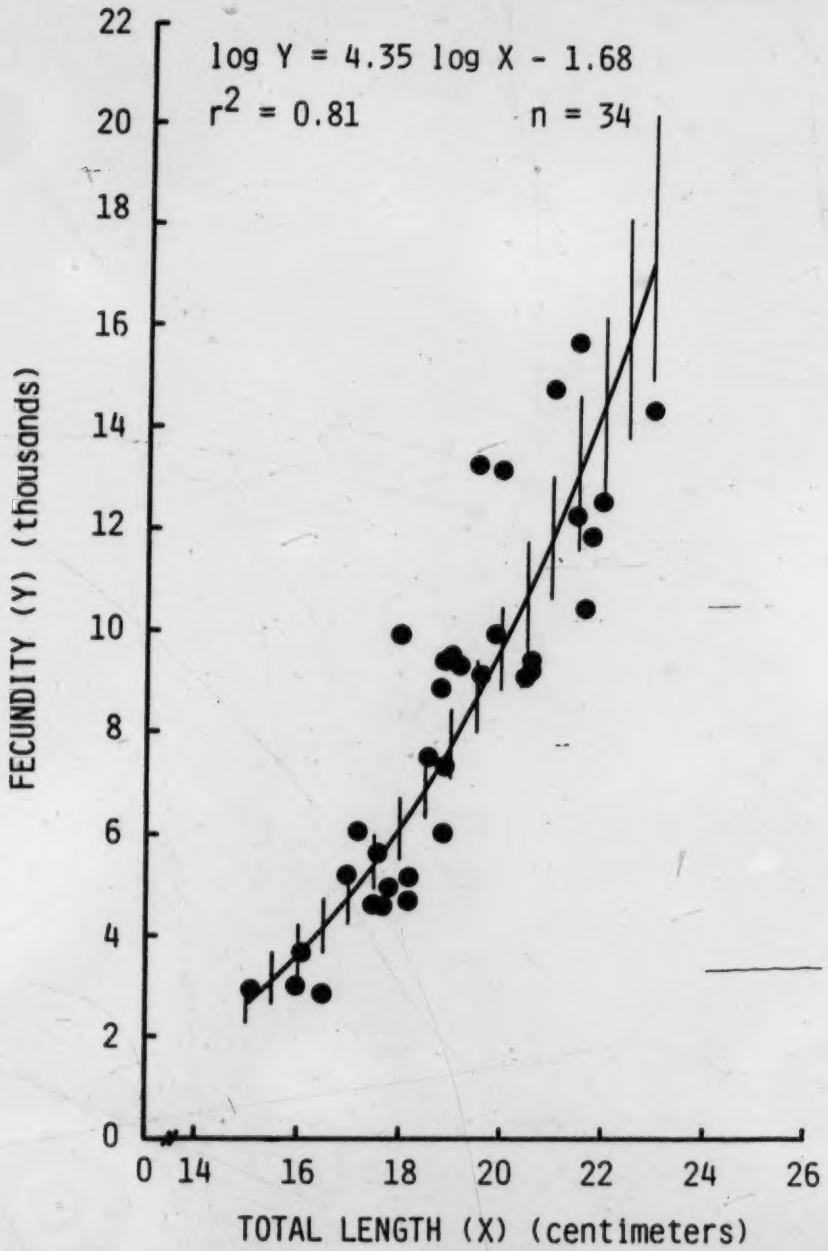
Appendix 1. Table 28. Two-way analysis of variance of the multiple regression of $\log_{10}$ fecundity (Y) on $\log_{10}$ somatic weight (X_1) and $\log_{10}$ age (X_2) for yellow perch collected from Narrow Lake on 23 February 1984.[1]

Term	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All slopes (b_i)	2	0.595607	0.297803	73.90	<0.001
Test of b_1 (somatic weight)	1	0.054808	0.054808	13.60	<0.001
Test of b_2 (age)	1	0.000040	0.000040	0.01	n.s.[2]
Error	6	0.024178	0.004030		
Total	8	0.619785			

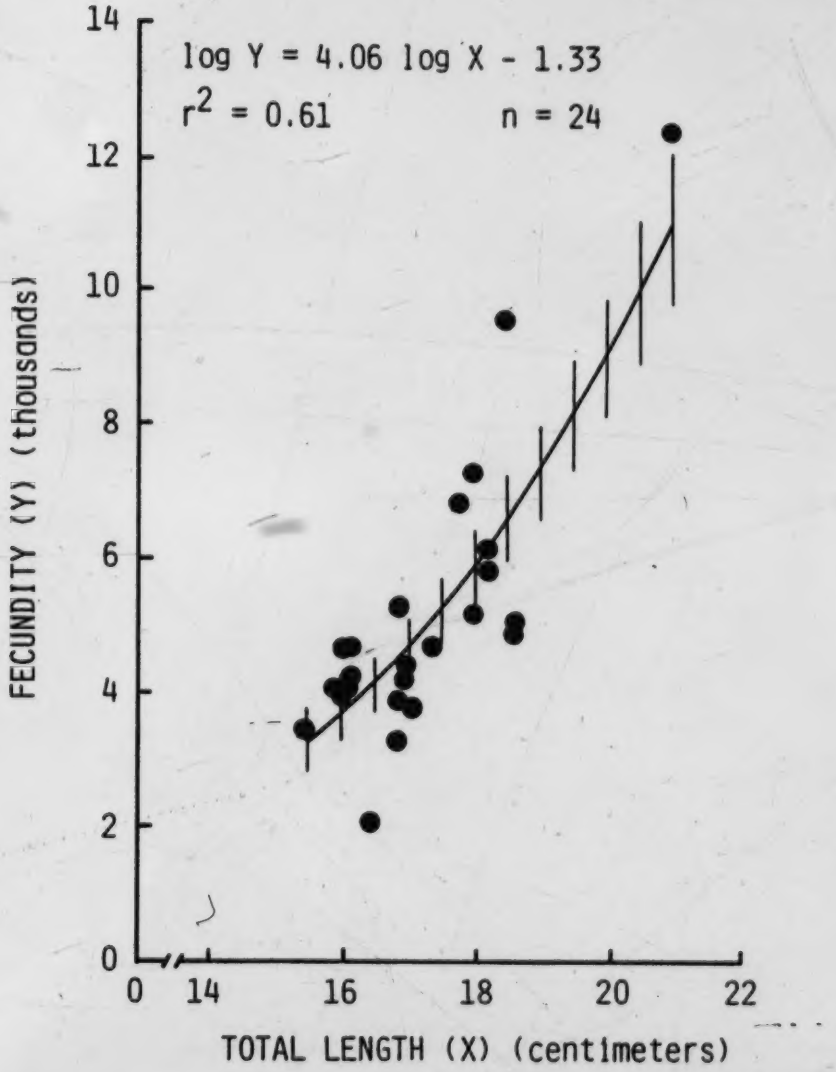
[1]Multiple regression equation: $\log_{10} Y = 2.0664 + \log_{10} X_1 + 0.0539 \log_{10} X_2$

Multiple correlation coefficient: r = 0.98

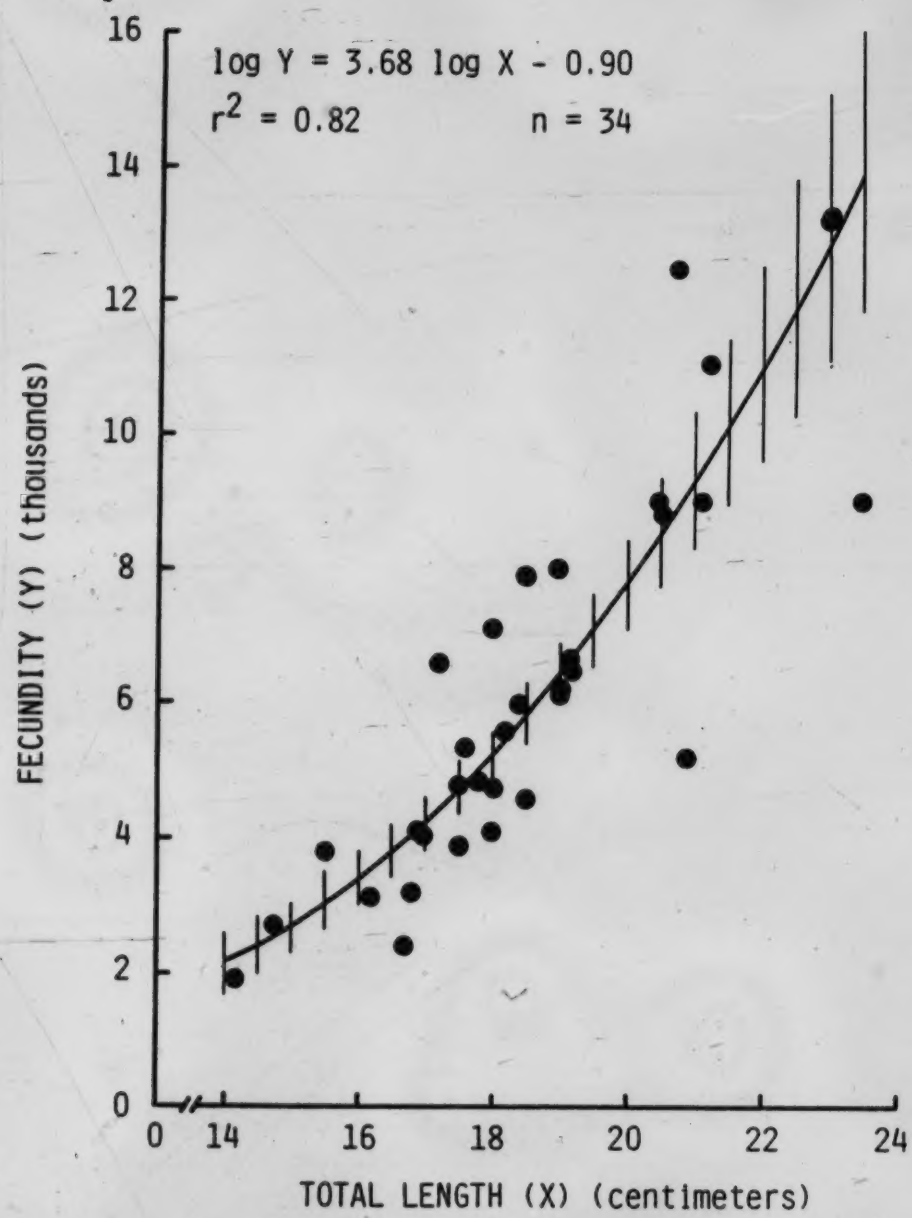
[2]n.s. - not significant



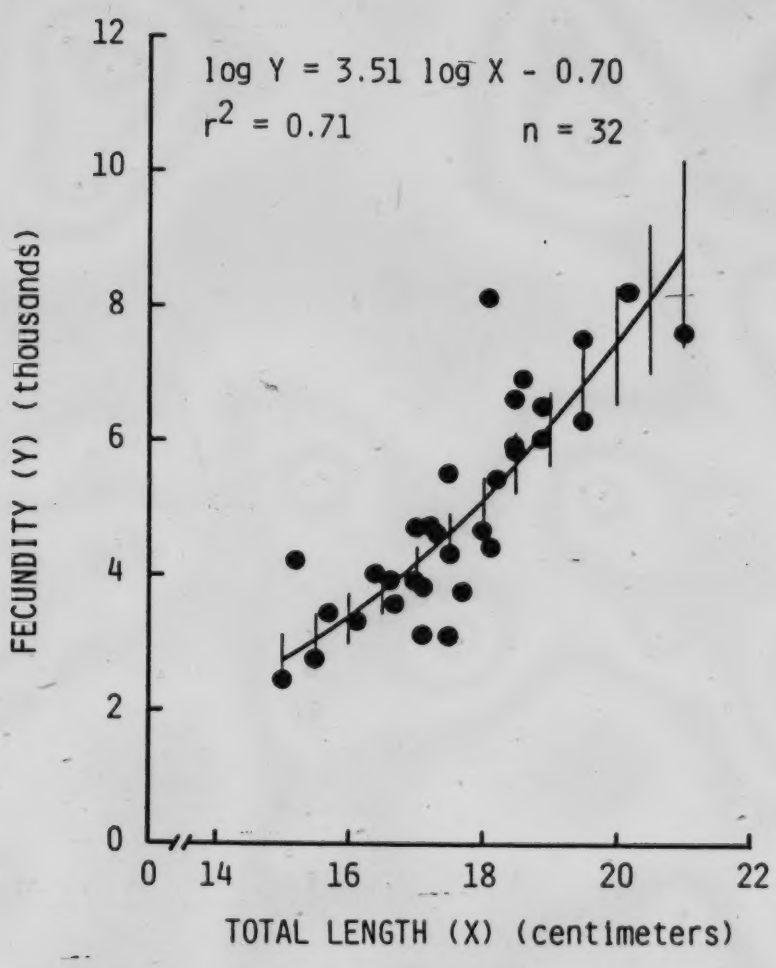
Appendix 2. Fig. 1. Scatter diagram of fecundity plotted against total length for yellow perch collected from Mayatan Lake, Alberta, on 8 October 1983. The shaded area corresponds to the 95% confidence limits of the regression estimates.



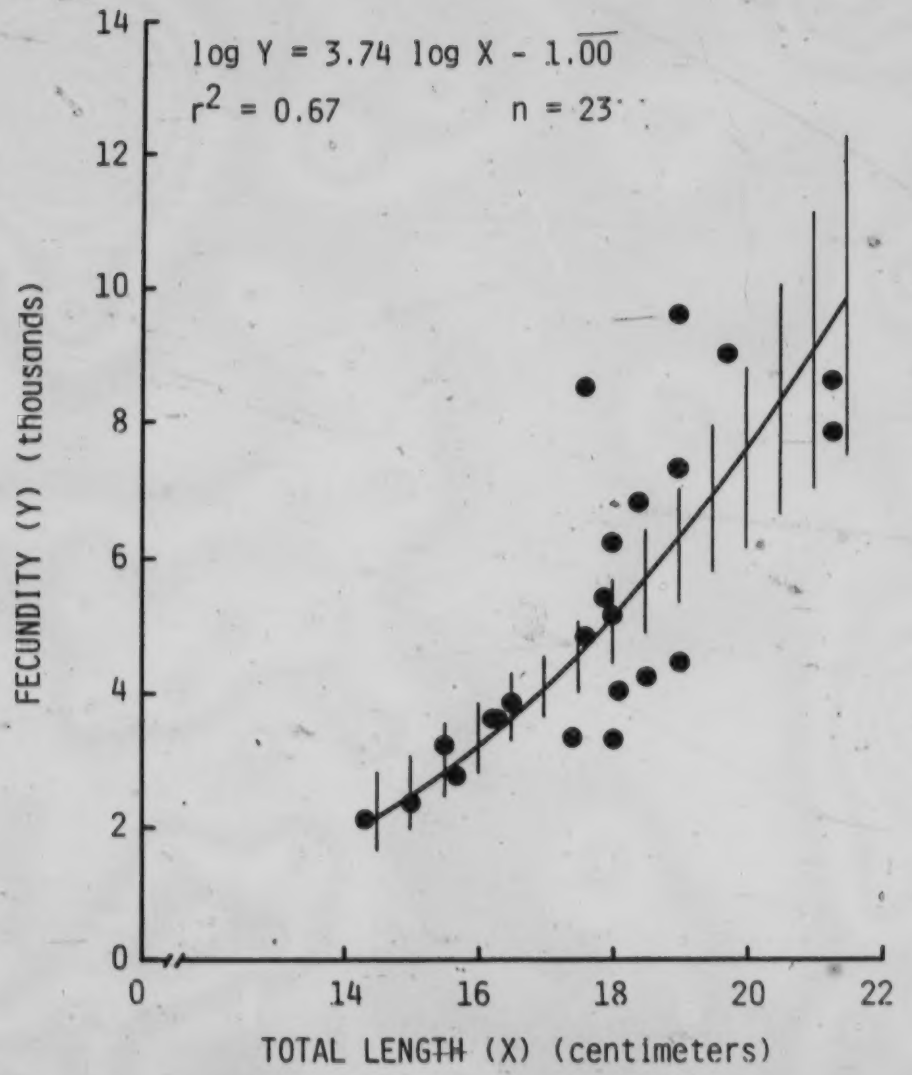
Appendix 2. Fig. 2. Scatter diagram of fecundity plotted against total length for yellow perch collected from Mayatan Lake, Alberta, on 5 December 1983. The shaded area corresponds to the 95% confidence limits of the regression estimates.



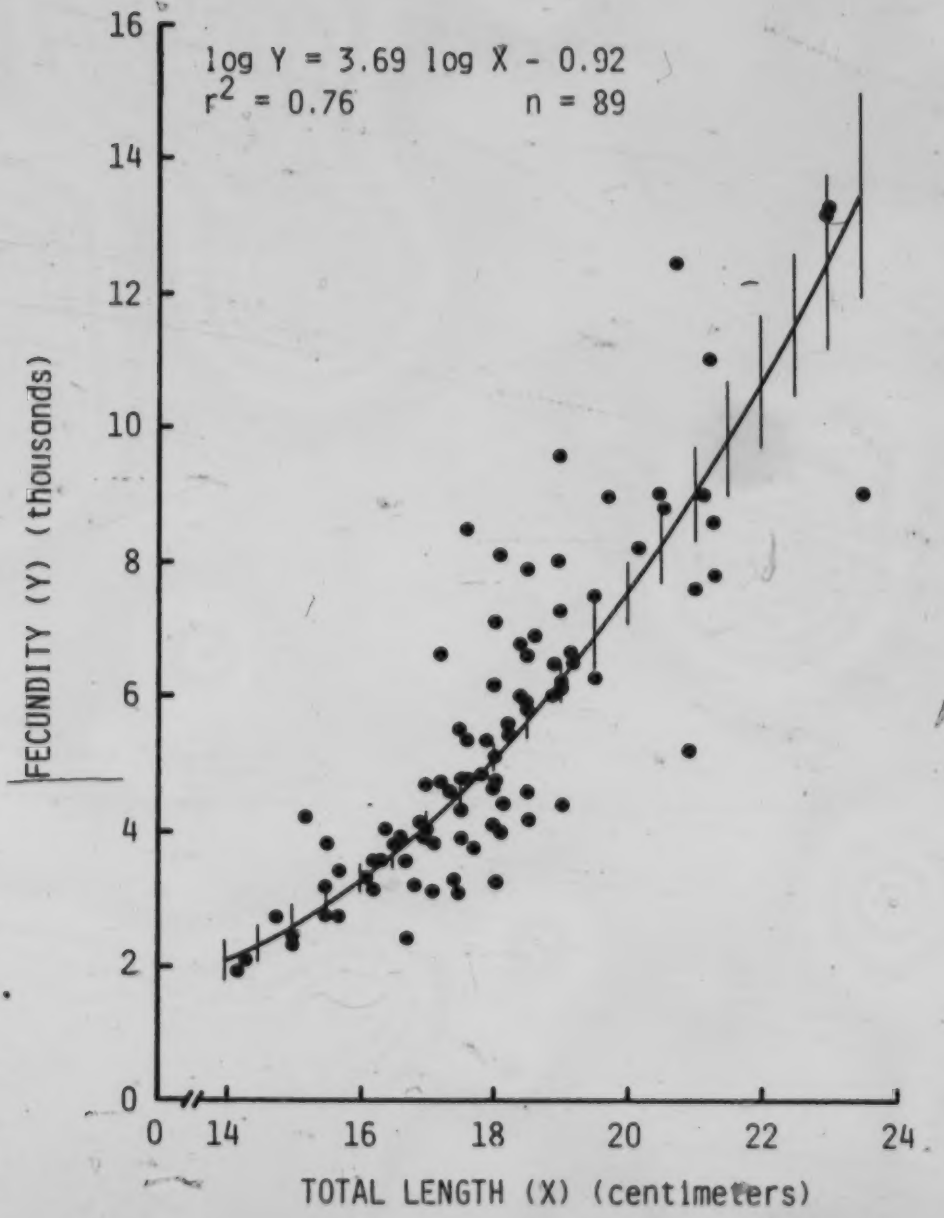
Appendix 2. Fig. 3. Scatter diagram of fecundity plotted against total length for yellow perch collected from Mayatan Lake, Alberta, on 14 & 28 January 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



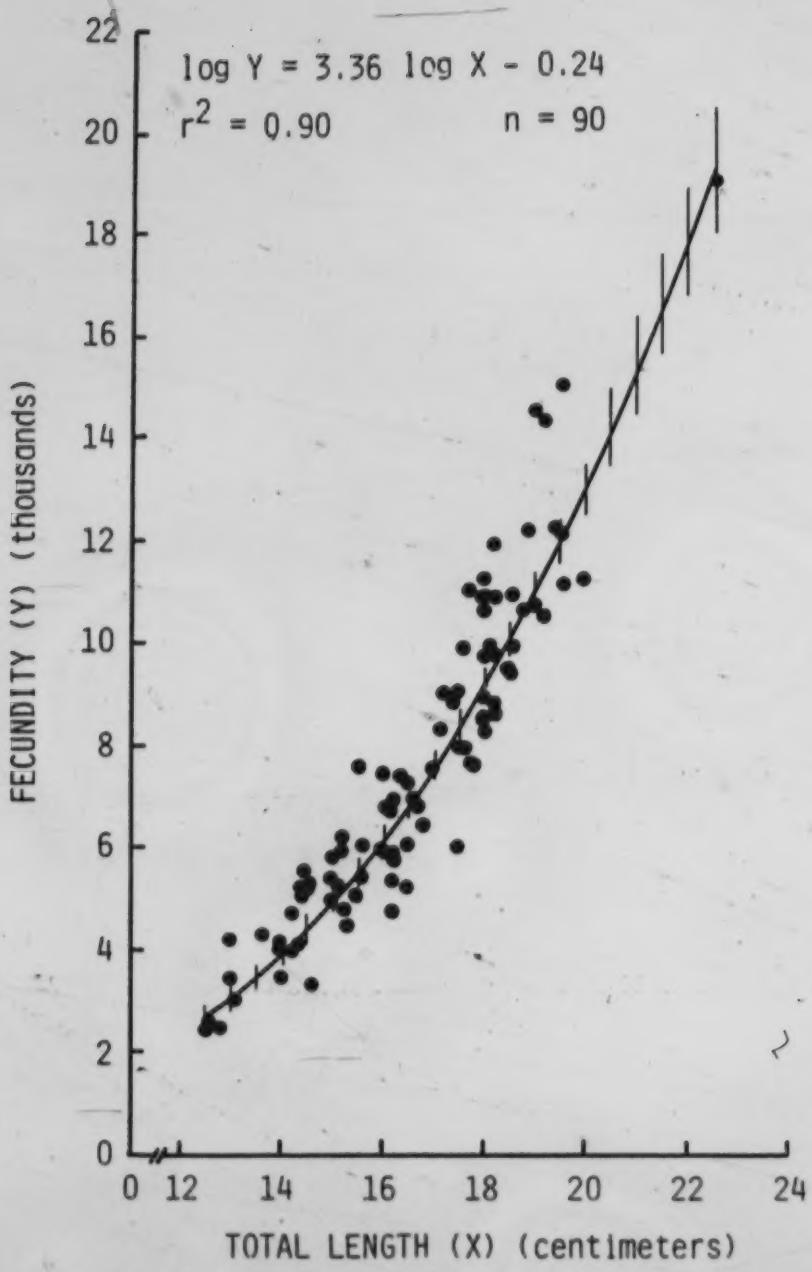
Appendix 2. Fig. 4. Scatter diagram of fecundity plotted against total length for yellow perch collected from Mayatan Lake, Alberta, on 27 February 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



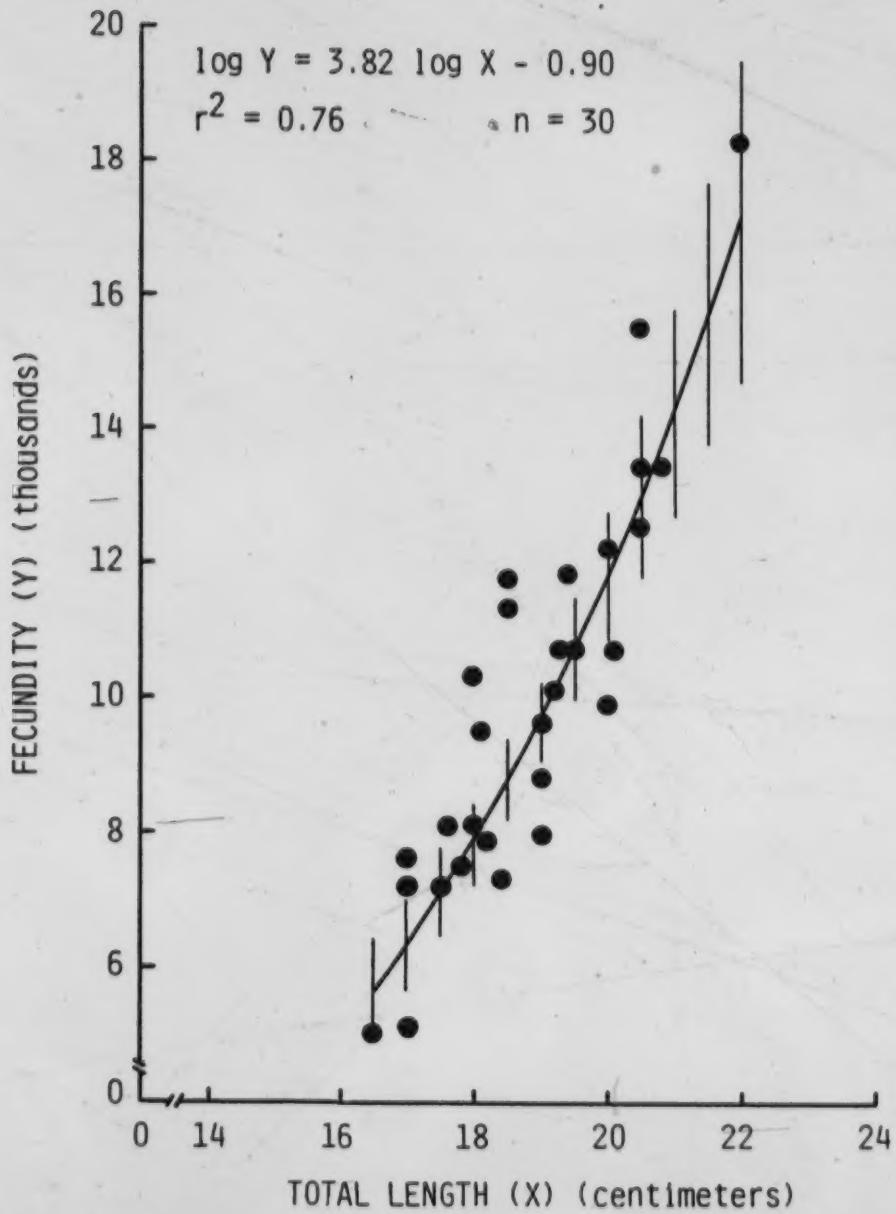
Appendix 2. Fig. 5. Scatter diagram of fecundity plotted against total length for yellow perch collected from Mayatan Lake, Alberta, on 15 March 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



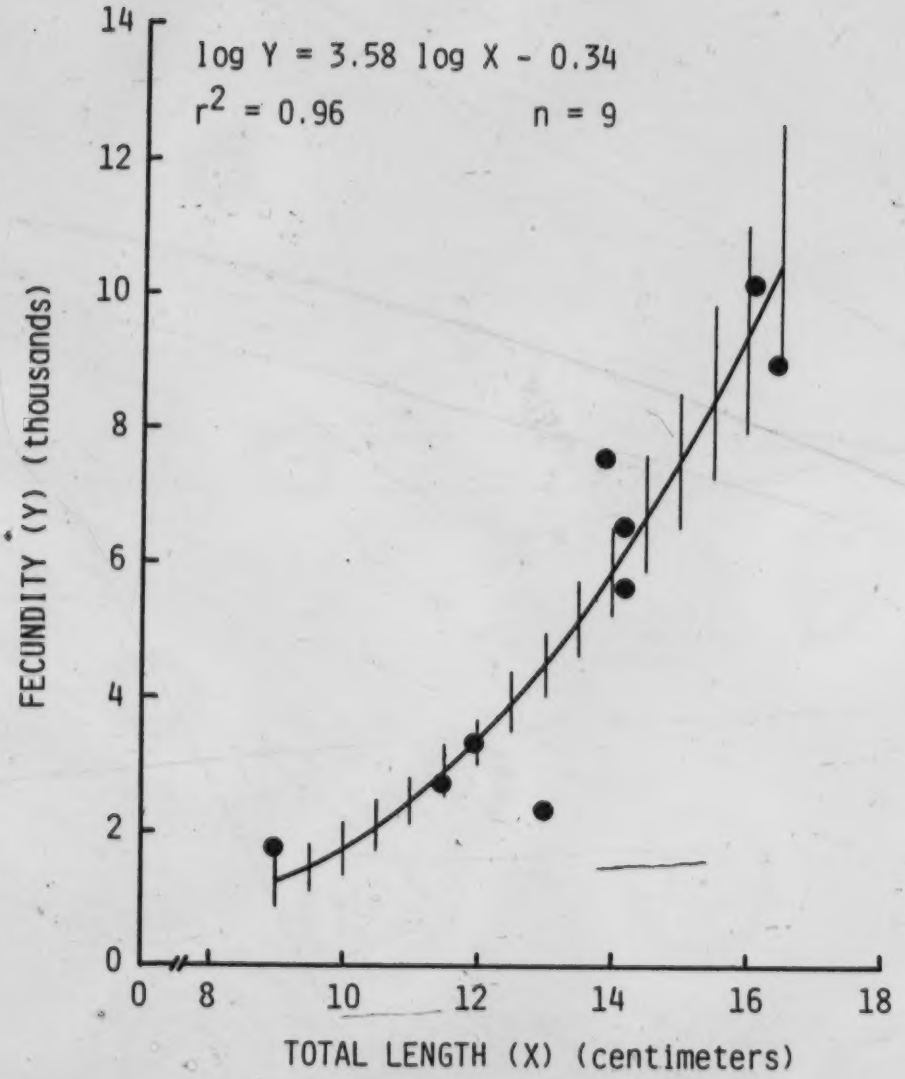
Appendix 2. Fig. 6. Scatter diagram of fecundity plotted against total length for yellow perch collected from Mayatan Lake, Alberta, between 14 January and 15 March 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



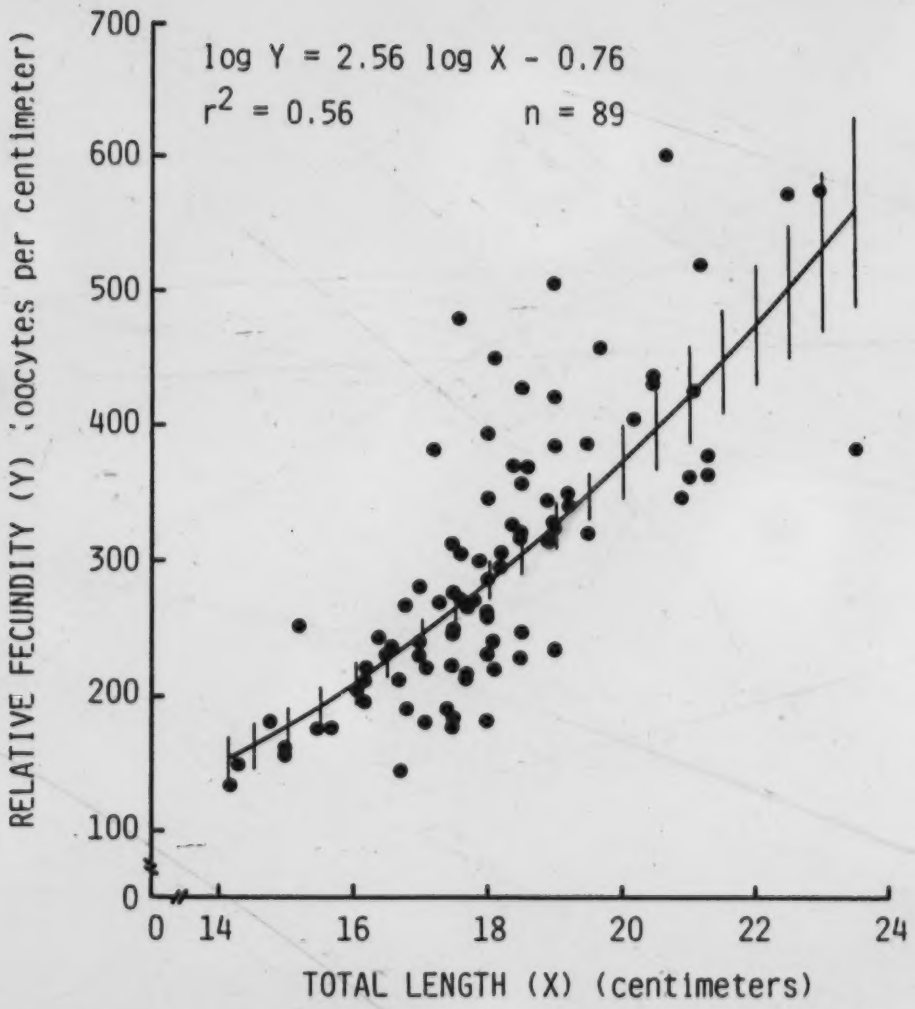
Appendix 2. Fig. 7. Scatter diagram of fecundity plotted against total length for yellow perch collected from Lac Ste. Anne on 23 February 1983 and 17 February 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



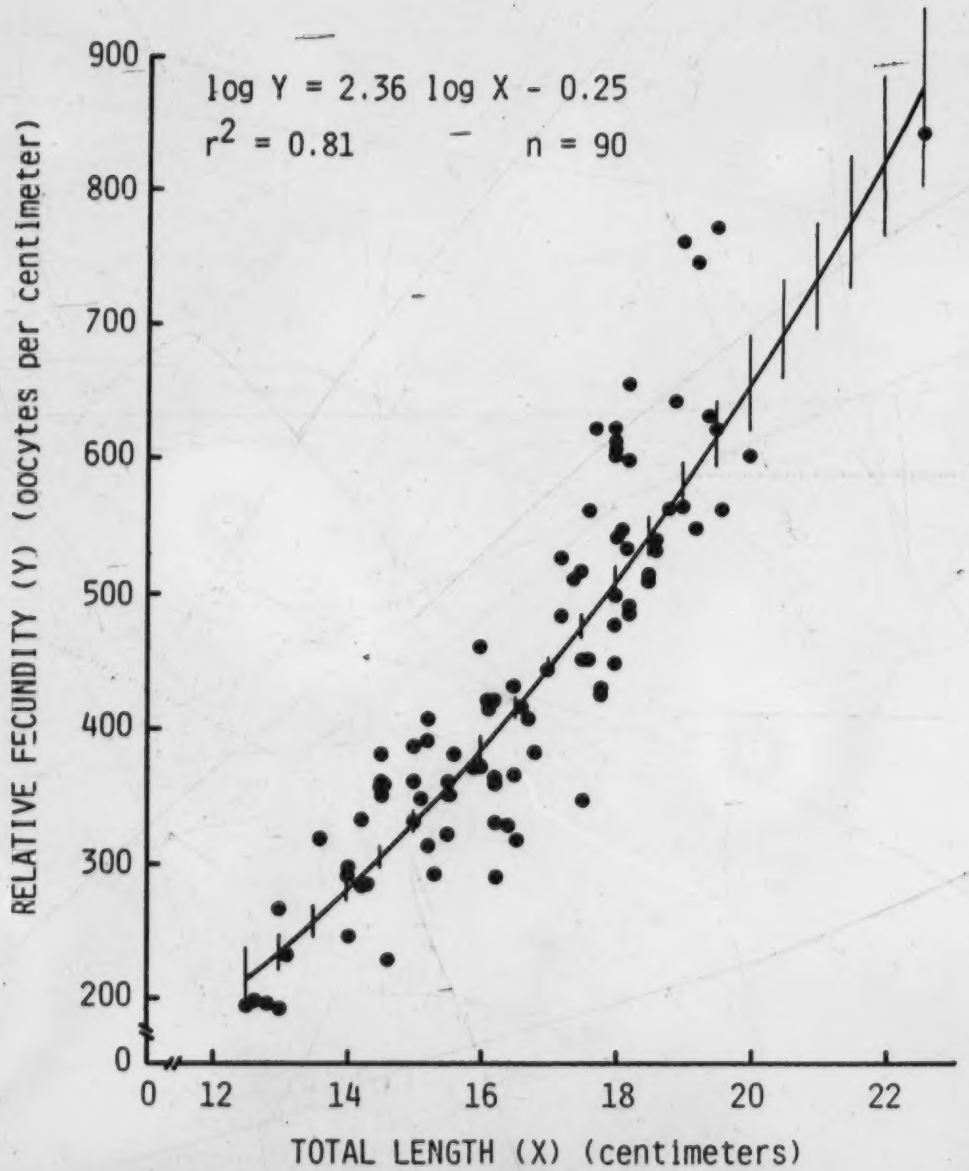
Appendix 2. Fig. 8. Scatter diagram of fecundity plotted against total length for yellow perch collected from Thunder Lake, Alberta, on 22 February 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



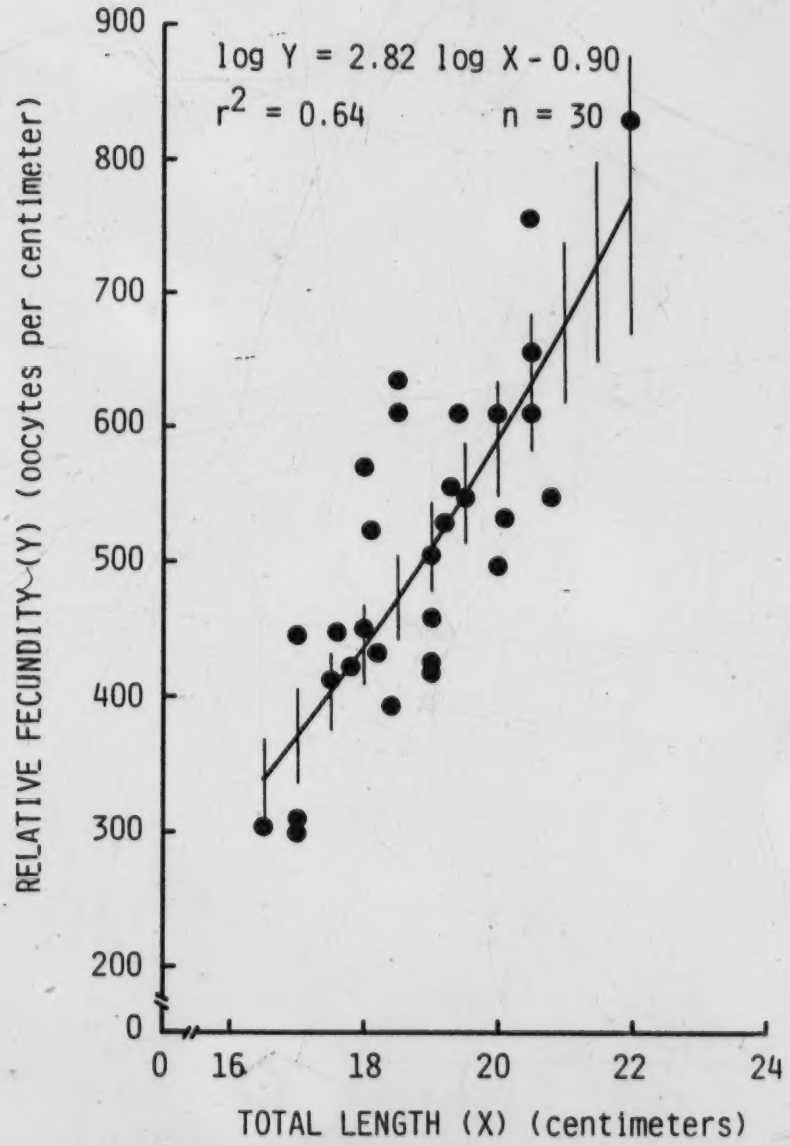
Appendix 2. Fig. 9. Scatter diagram of fecundity plotted against total length for yellow perch collected from Narrow Lake, Alberta, on 23 February 1984. The shaded area corresponds to 95% confidence limits of the regression estimates.



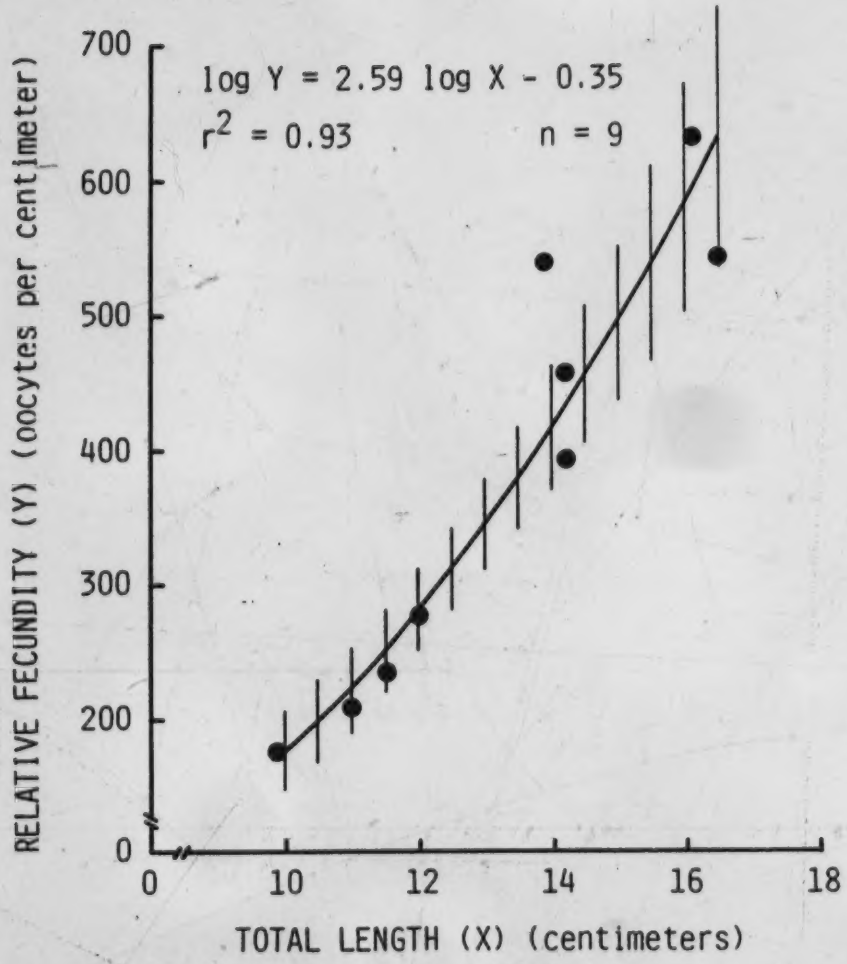
Appendix 2. Fig. 10. Scatter diagram of length-specific fecundity plotted against total length for yellow perch collected from Mayatan Lake, Alberta, between 14 January and 15 March 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



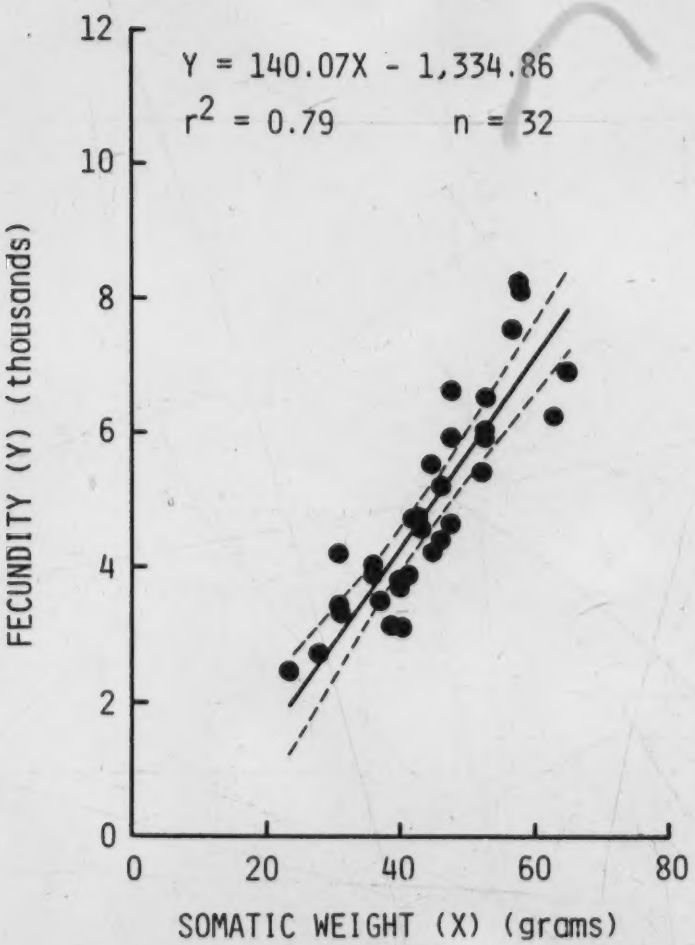
Appendix 2. Fig. 11. Scatter diagram of length-specific fecundity plotted against total length for yellow perch collected from Lac Ste. Anne, Alberta, on 23 February 1983 and 17 February 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



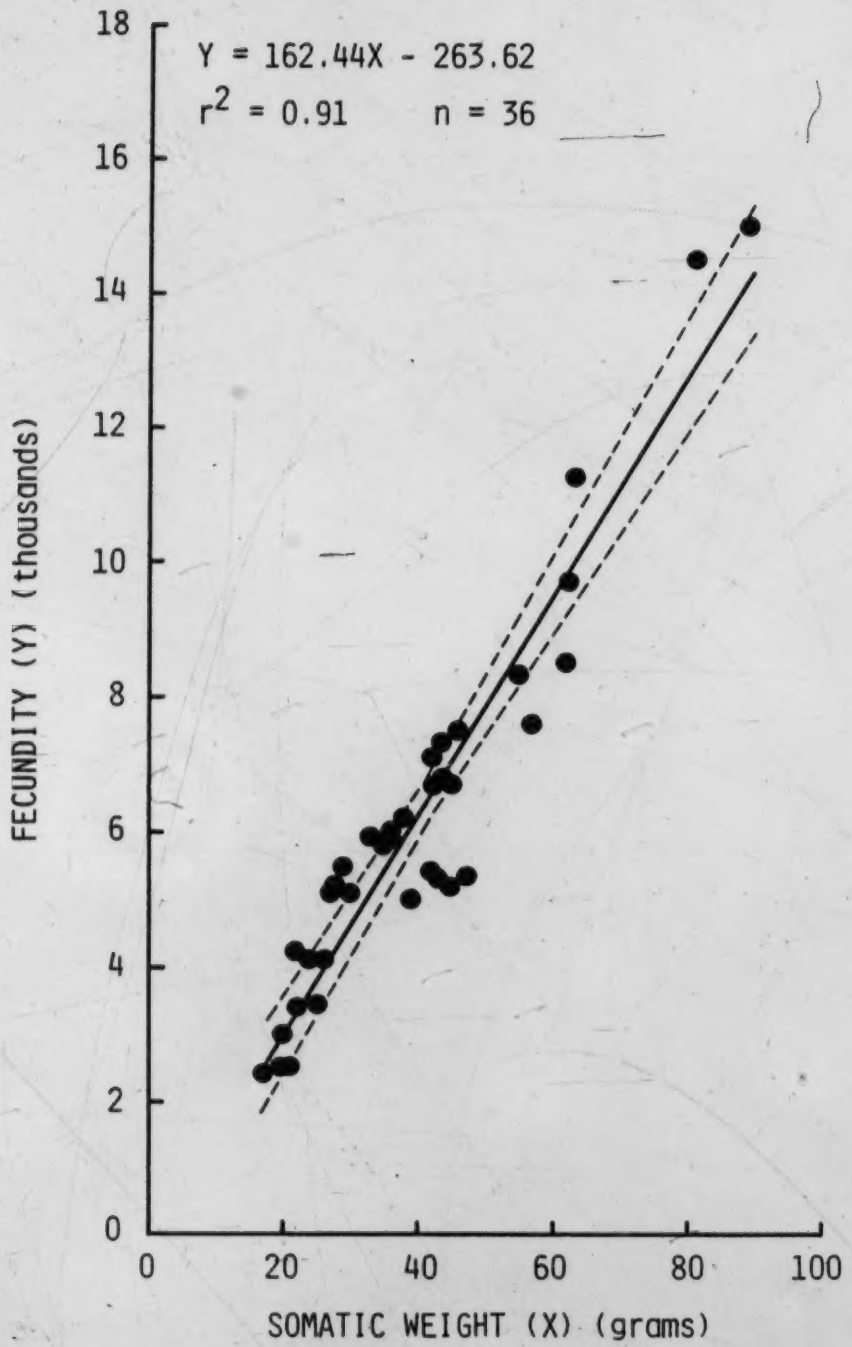
Appendix 2. Fig. 12. Scatter diagram of length-specific fecundity plotted against total length for yellow perch collected from Thunder Lake on 22 February 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



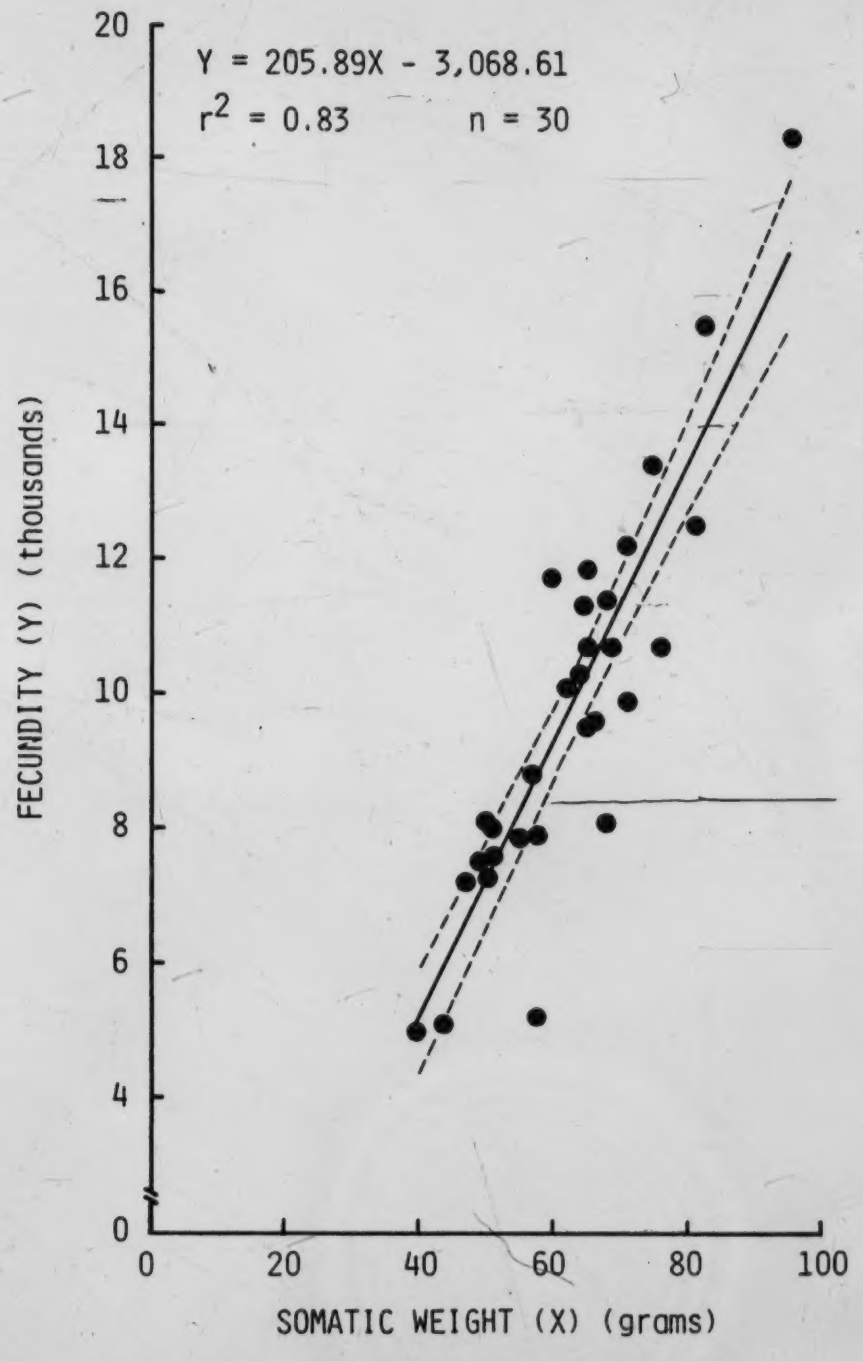
Appendix 2. Fig. 13. Scatter diagram of length-specific fecundity plotted against total length for yellow perch collected from Narrow Lake, Alberta, on 23 February 1984. The shaded area corresponds to the 95% confidence limits of the regression estimates.



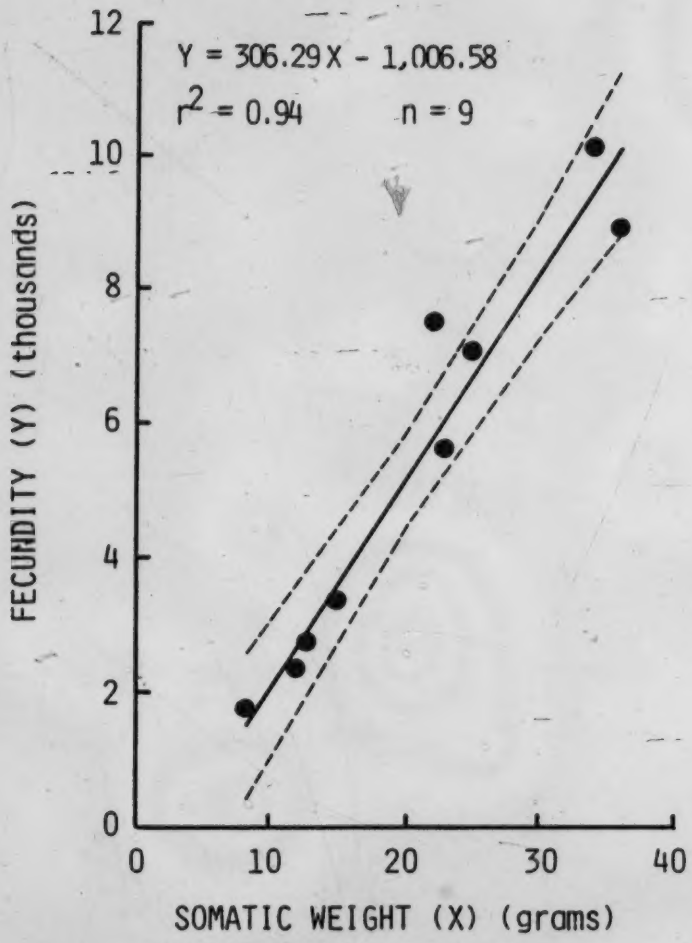
Appendix 2. Fig. 14. Scatter diagram of fecundity plotted against somatic weight for yellow perch collected from Mayatan Lake, Alberta, on 27 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



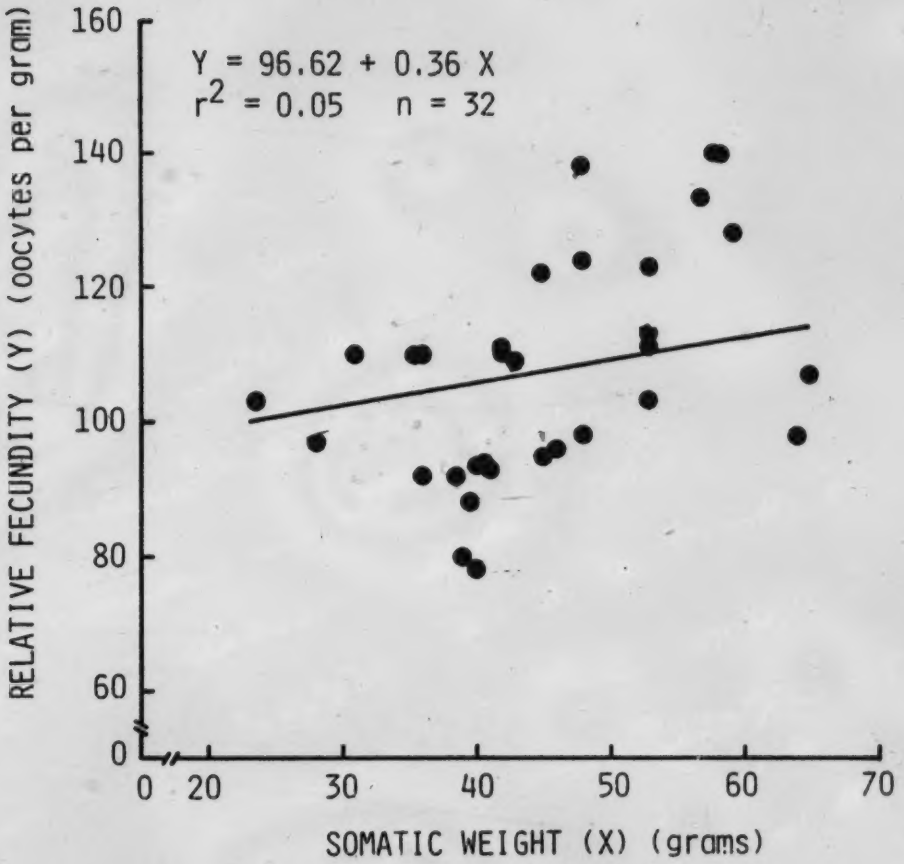
Appendix 2. Fig. 15. Scatter diagram of fecundity plotted against somatic weight for yellow perch collected from Lac Ste. Anne, Alberta, on 17 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



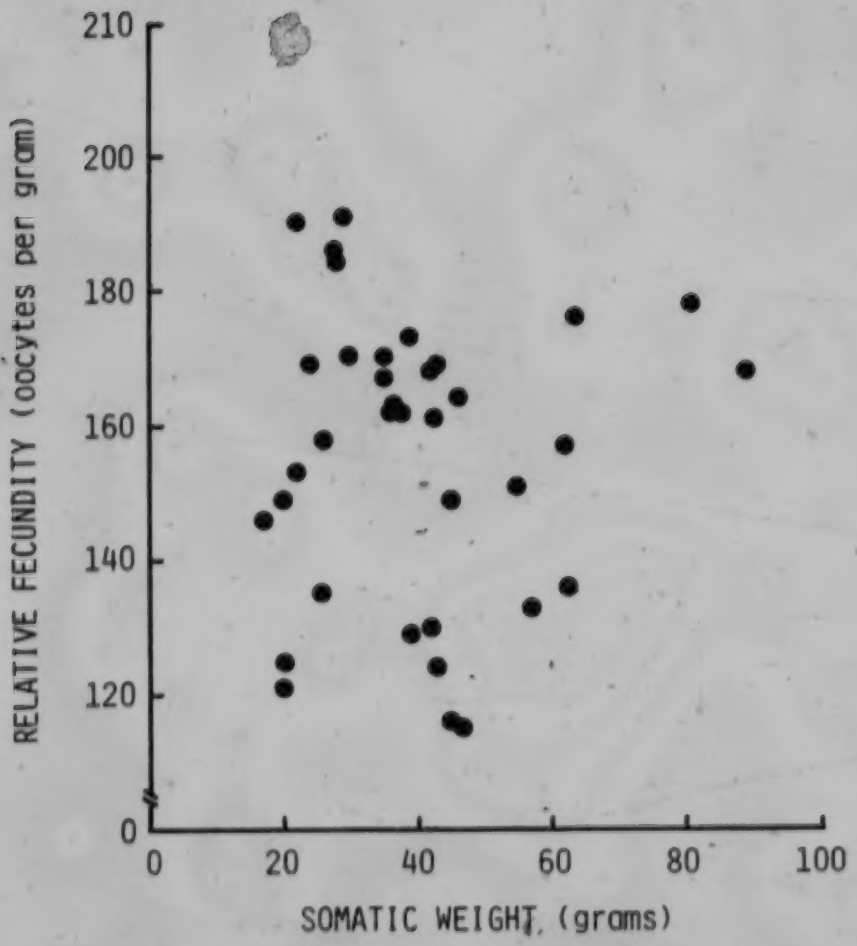
Appendix 2. Fig. 16. Scatter diagram of fecundity plotted against somatic weight for yellow perch collected from Thunder Lake, Alberta, on 22 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



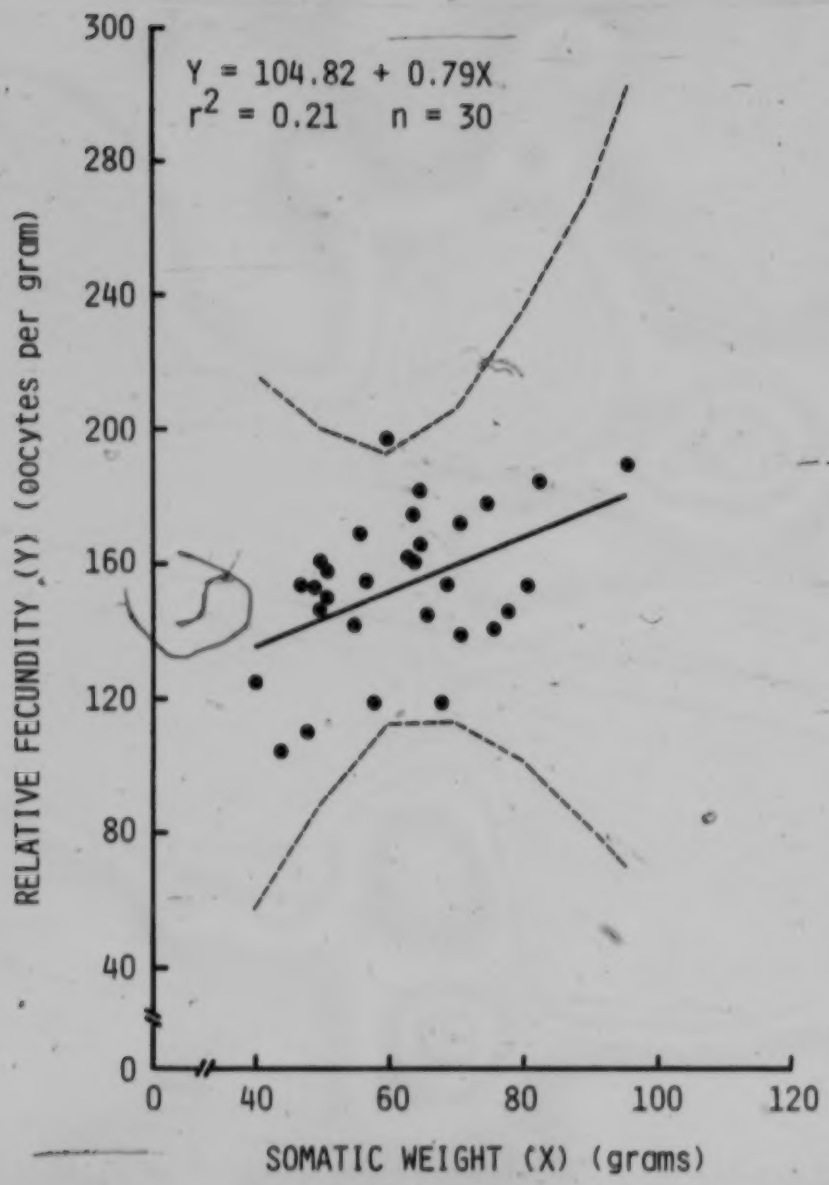
Appendix 2. Fig. 17. Scatter diagram of fecundity plotted against somatic weight for yellow perch collected from Narrow Lake, Alberta, on 23 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



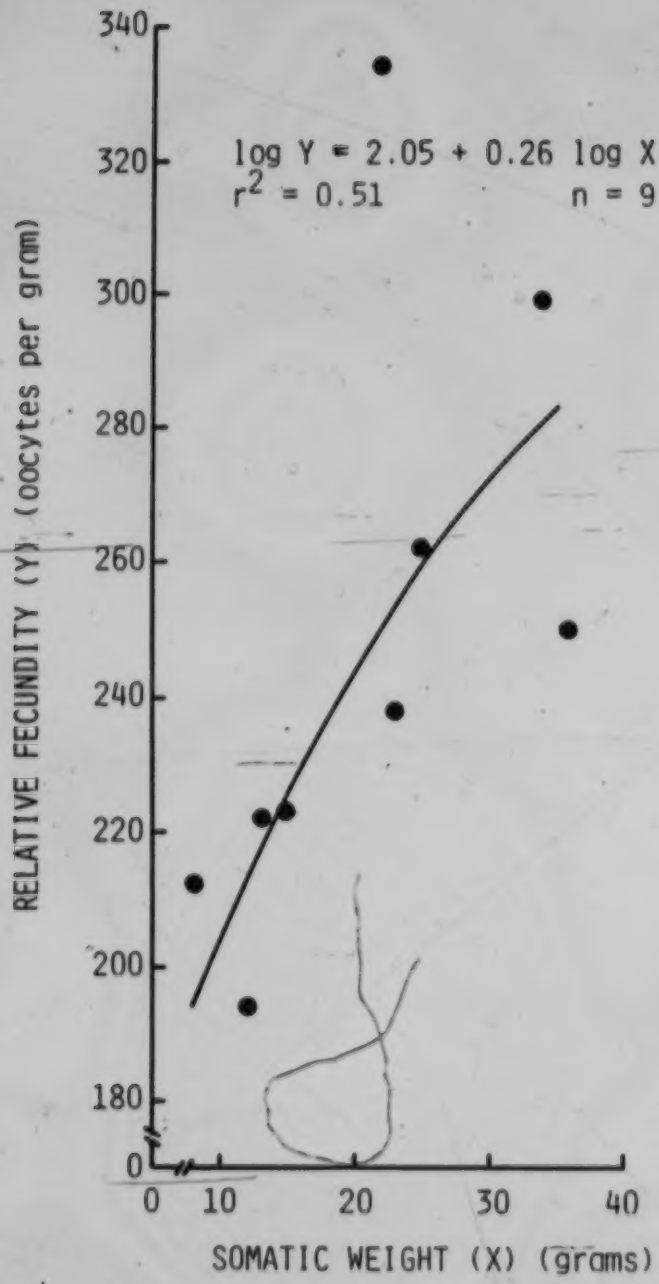
Appendix 2. Fig. 18. Scatter diagram of somatic-weight-specific fecundity plotted against somatic weight for yellow perch collected from Mayatan Lake, Alberta, on 27 February 1984. The F value for the analysis of variance of relative fecundity on somatic weight regression is not significant at the 5% level.



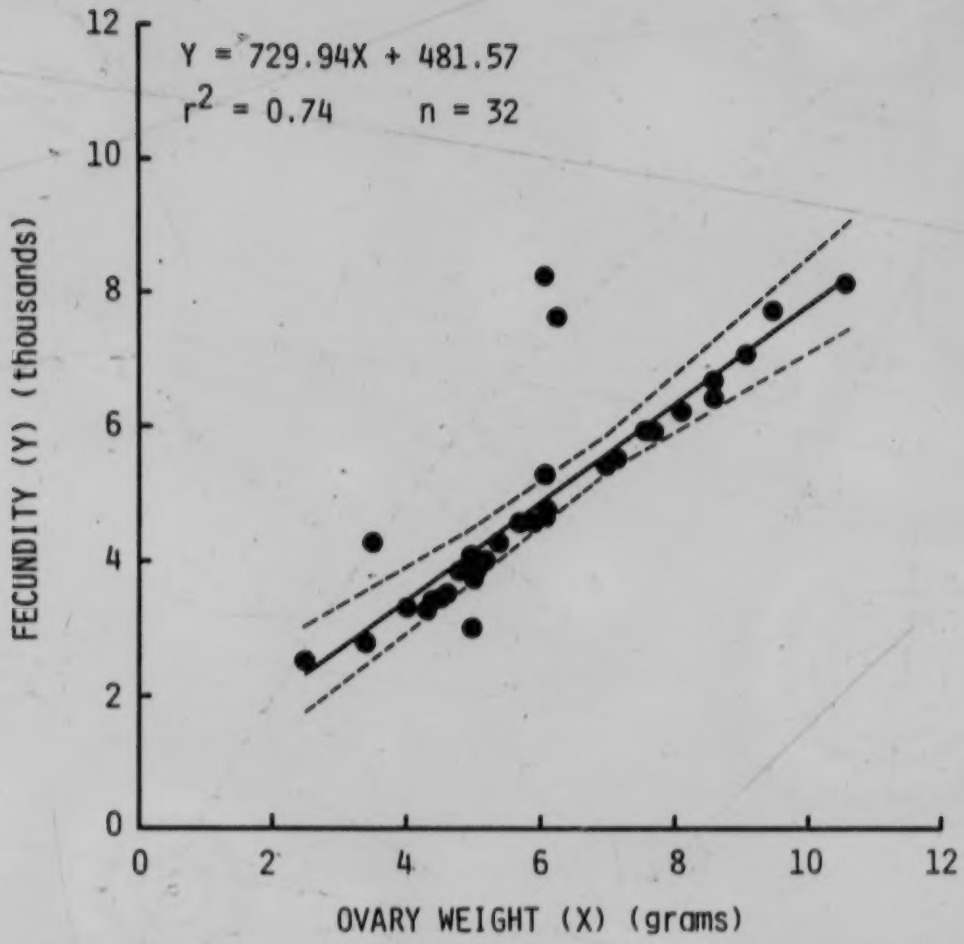
Appendix 2. Fig. 19. Scatter diagram of somatic-weight-specific fecundity and somatic weight for yellow perch collected from Lac Ste. Anne, Alberta, on 17 February 1984. There is no apparent relationship between the two variates.



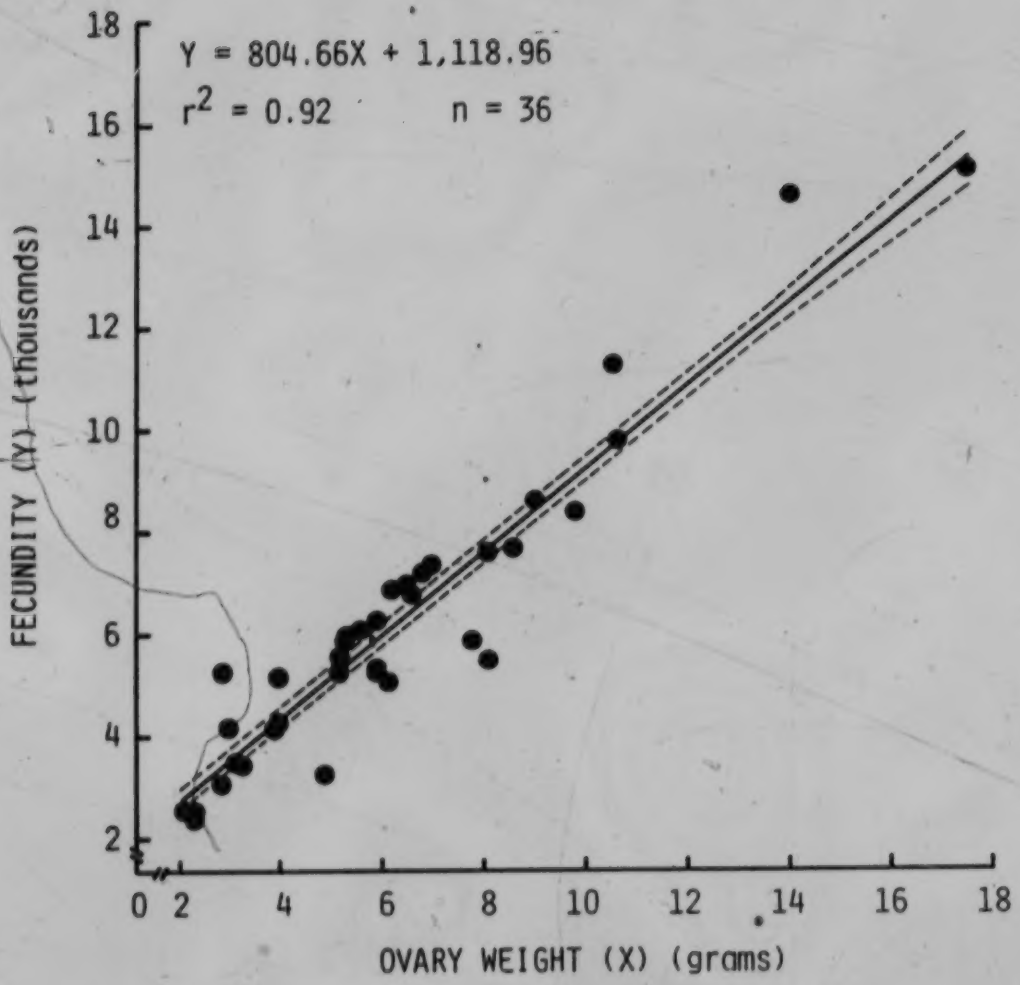
Appendix 2. Fig. 20. Scatter diagram of somatic-weight-specific fecundity plotted against somatic weight for yellow perch collected from Thunder Lake, Alberta, on 22 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



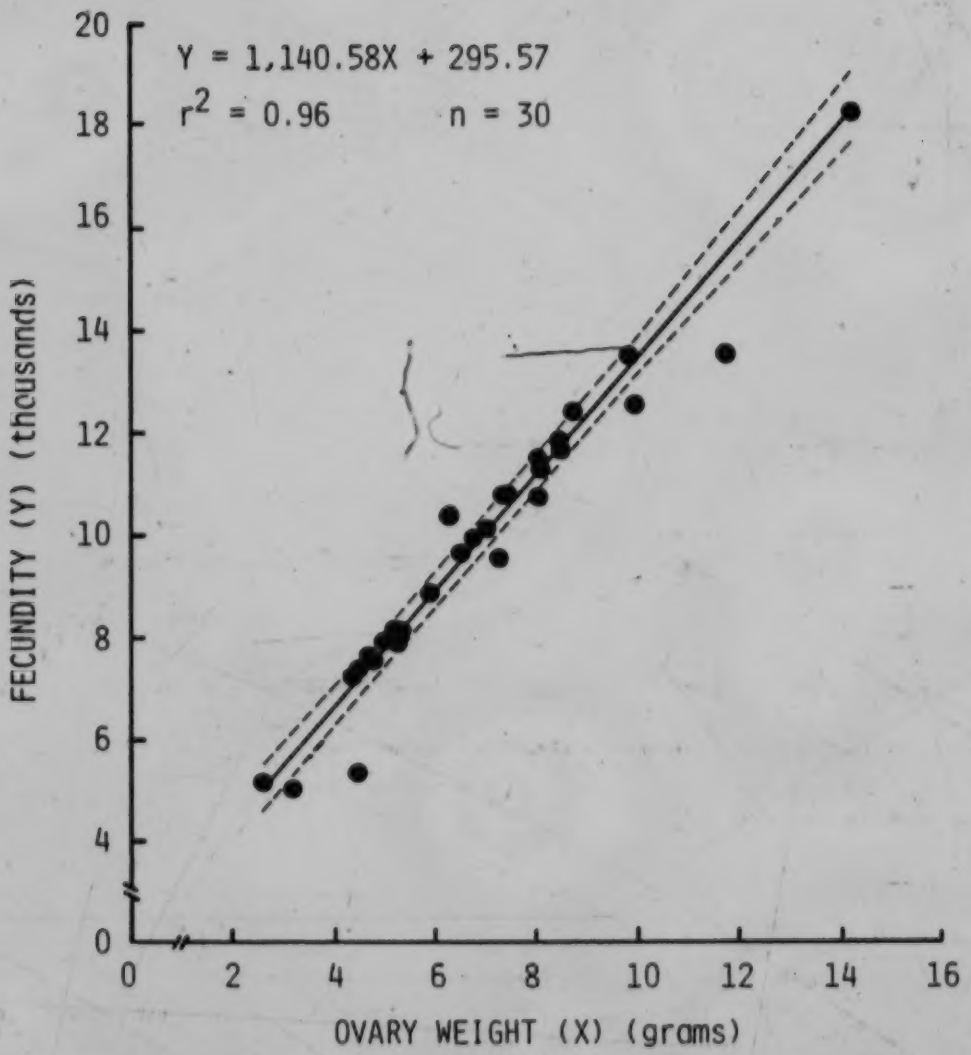
Appendix 2. Fig. 21. Scatter diagram of somatic-weight-specific fecundity plotted against somatic weight for yellow perch collected from Narrow Lake, Alberta, on 23 February 1984. The F value for the analysis of variance of relative fecundity on somatic weight regression is not significant at the 5% level.



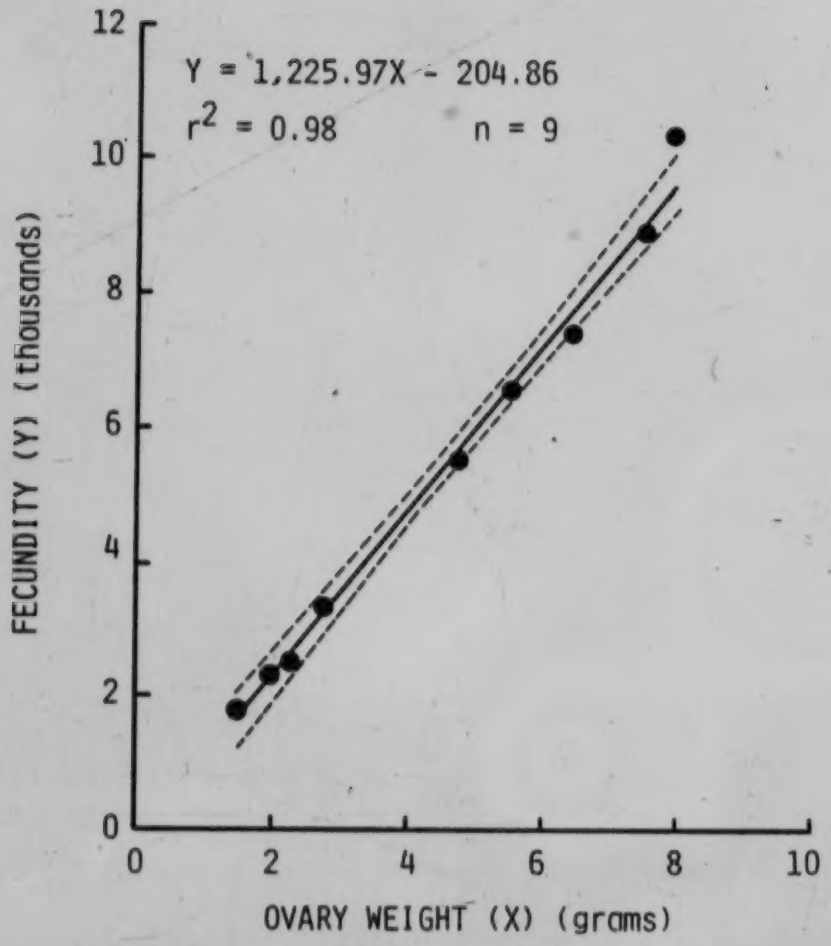
Appendix 2. Fig. 22. Scatter diagram of fecundity plotted against ovary weight for yellow perch collected from Mayatan Lake, Alberta, on 27 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



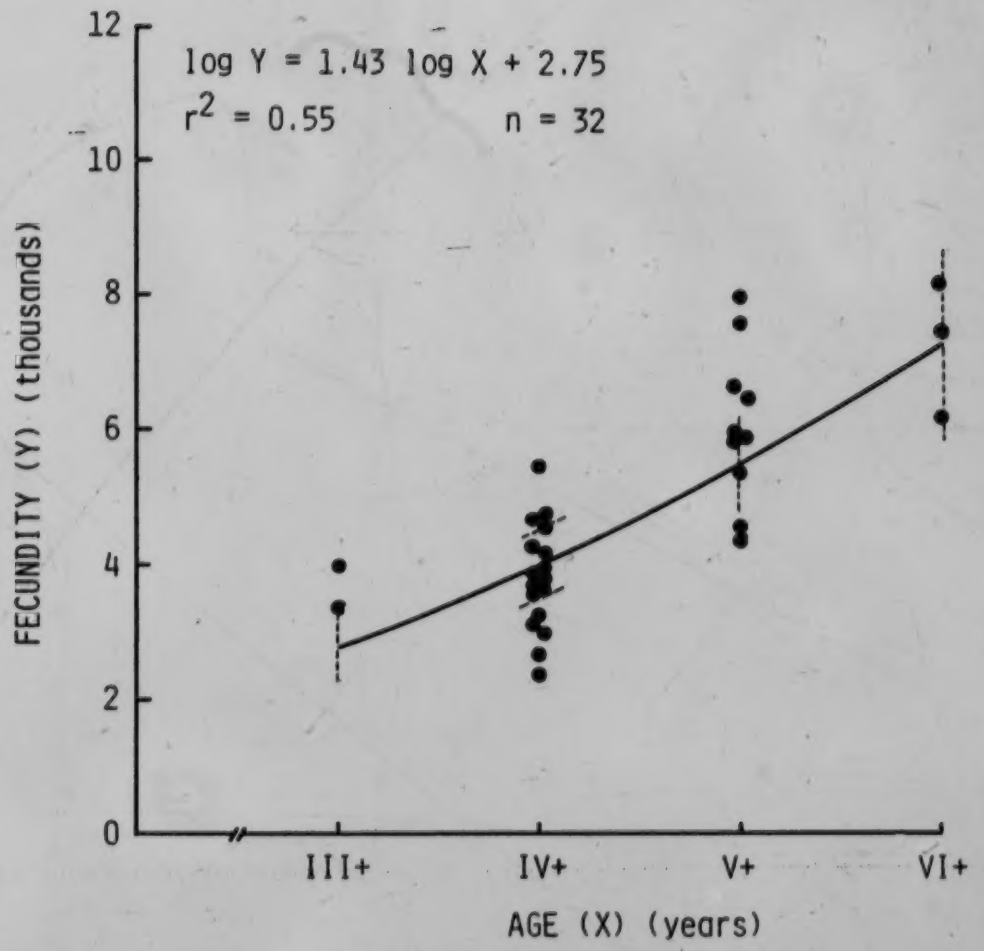
Appendix 2. Fig. 23. Scatter diagram of fecundity plotted against ovary weight for yellow perch collected from Lac Ste. Anne, Alberta, on 17 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



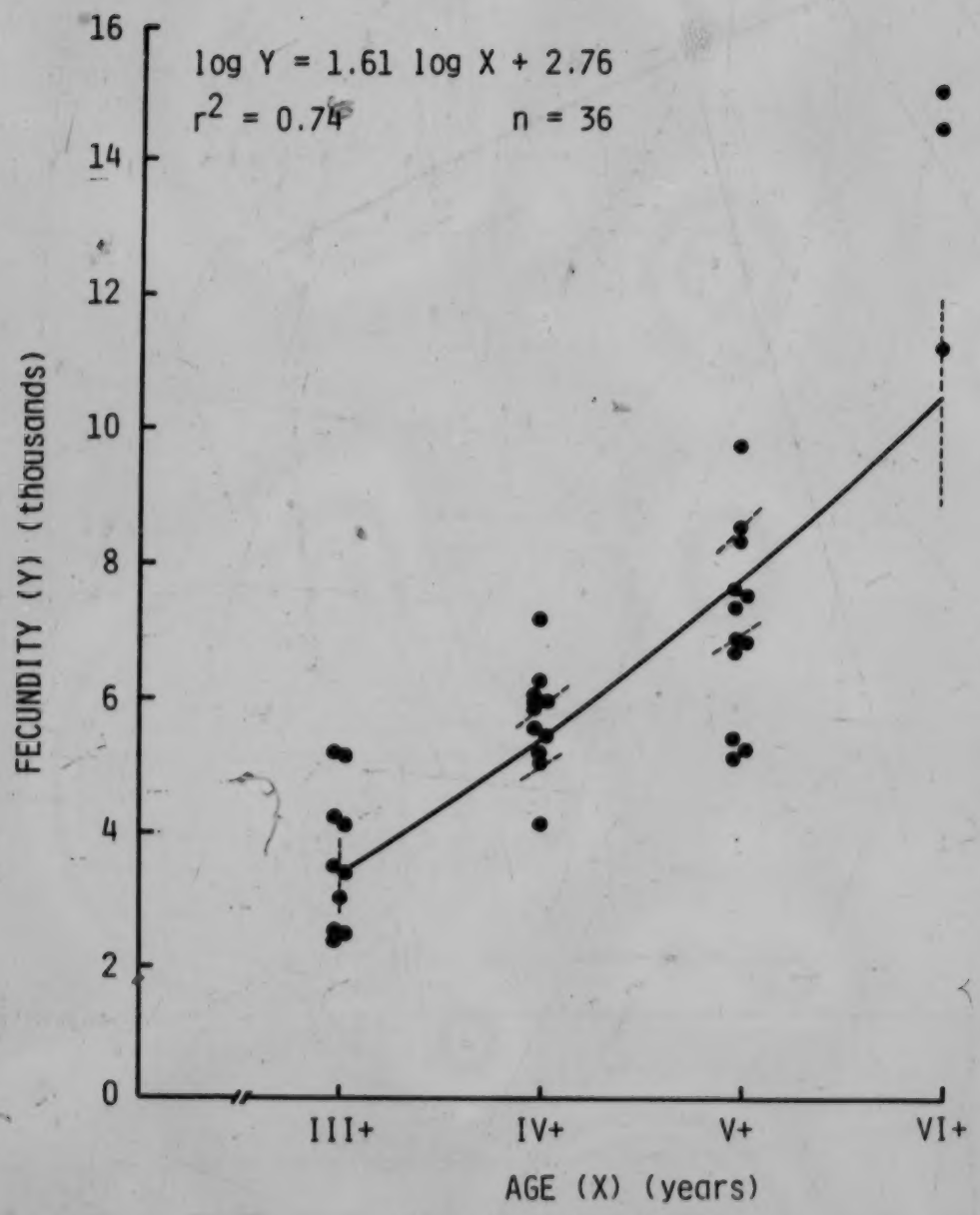
Appendix 2. Fig. 24. Scatter diagram of fecundity plotted against ovary weight for yellow perch collected from Thunder Lake, Alberta, on 22 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



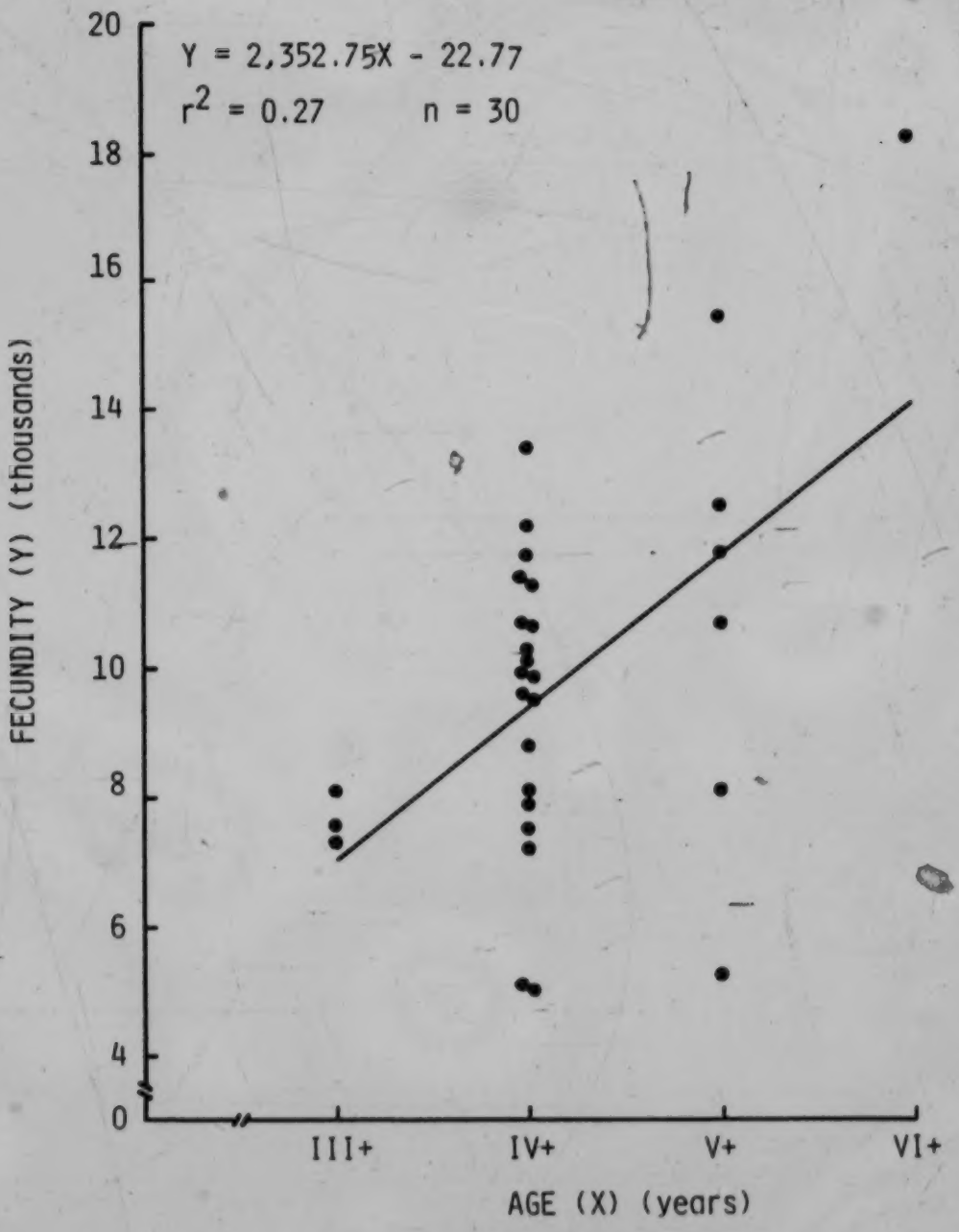
Appendix 2. Fig. 25. Scatter diagram of fecundity plotted against ovary weight for yellow perch collected from Narrow Lake, Alberta, on 23 February 1984. The broken lines represent the 95% confidence limits to the regression estimates.



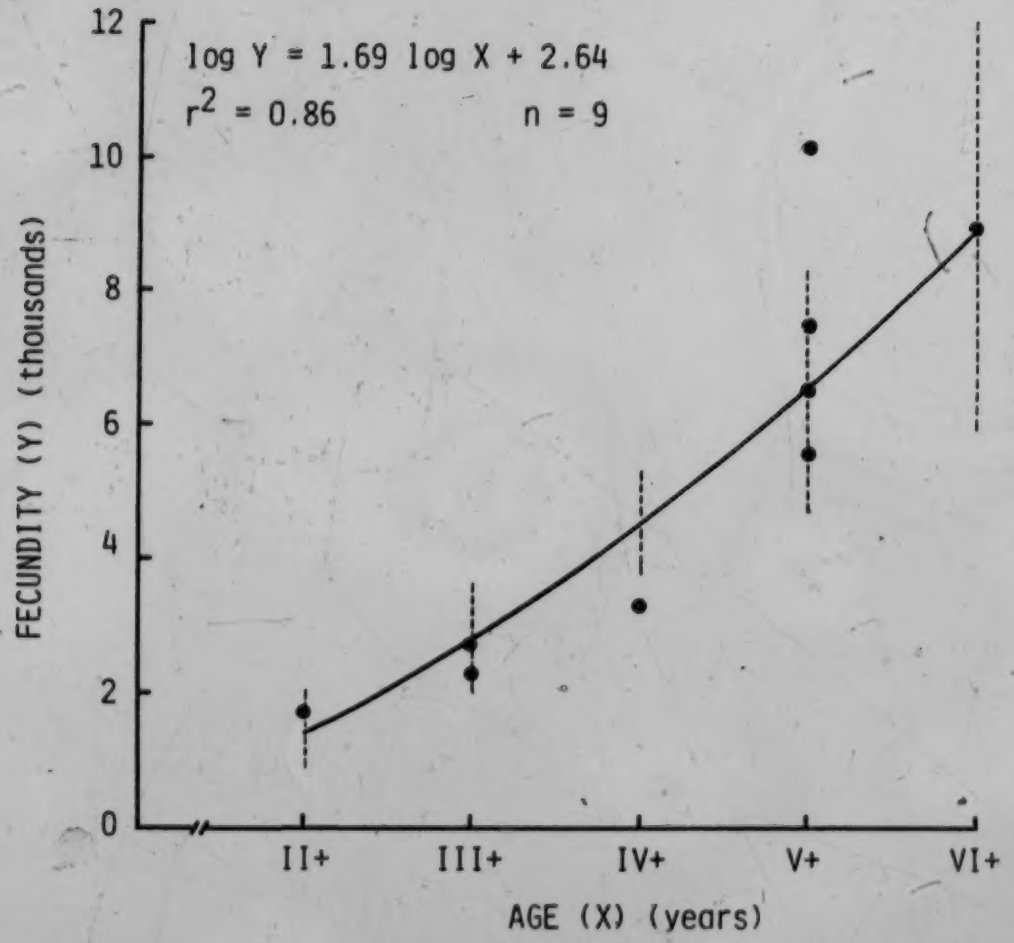
Appendix 2. Fig. 26. Scatter diagram of fecundity plotted against age for yellow perch collected from Mayatan Lake, Alberta, on 27 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



Appendix 2. Fig. 27. Scatter diagram of fecundity plotted against age for yellow perch collected from Lac Ste. Anne, Alberta, on 17 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.



Appendix 2. Fig. 28. Scatter diagram of fecundity plotted against age for yellow perch collected from Thunder Lake, Alberta, on 22 February 1984. The 95% confidence limits for the fecundity estimate at age III+ is ± 10,633, age IV+ is ± 5,262, age V+ is ± 8,350, and age VI+ is ± 15,466.



Appendix 2. Fig. 29. Scatter diagram of fecundity plotted against age for yellow perch collected from Narrow Lake, Alberta, on 23 February 1984. The broken lines represent the 95% confidence limits of the regression estimates.

Appendix 3. Table 1. Data for female yellow perch collected from Mayatan Lake, Alberta, on 8 October 1983.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes		GSI
						per cm	per gm	
83146	21.5	76.65	4.93	VII+	15,651	728	204	6.43
83148	23.0	99.86	5.02	VII+	14,316	622	143	5.03
83149	19.5	79.23	4.81	VII+	13,256	689	167	6.07
83150	20.0	72.01	4.13	VI+	13,111	656	182	5.74
83151	18.8	55.15	2.62	VI+	8,845	470	160	4.75
83153	22.0	95.89	3.94	VII+	12,508	130	160	4.11
83154	18.2	49.39	1.51	VI+	4,715	259	95	3.06
83157	19.0	64.95	2.98	VII+	9,460	498	146	4.59
83159	18.9	59.83	2.43	VI+	7,364	392	124	4.06
83160	17.6	40.69	1.77	V+	5,589	318	137	4.35
83161	18.2	52.46	1.55	VI+	5,146	283	98	2.95
83166	17.5	45.03	1.62	V+	4,604	263	102	3.60
83167	21.5	83.10	2.41	VI+	12,229	569	147	2.90
83169	20.6	69.96	3.39	VI+	9,425	457	135	4.85
83170	18.9	56.87	2.13	VI+	6,013	318	106	3.75
83171	20.6	69.41	2.77	VI+	9,183	446	132	3.99
83172	16.1	30.71	1.46	IV+	3,657	227	119	4.75
83175	21.7	77.91	3.01	VII+	10,402	479	133	3.86
83176	19.6	60.48	2.86	VI+	9,079	463	150	4.73
83177	18.6	53.31	2.19	VI+	7,504	403	141	4.11
83178	21.2	81.73	3.73	VII+	11,809	557	144	4.56
83179	19.9	62.56	2.80	VI+	9,921	498	159	4.48
83180	21.0	79.29	4.63	VII+	14,698	700	185	5.84
83181	19.2	60.62	2.94	V+	9,323	486	154	4.85

Appendix 3. Table II... continuation

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
83184	20.5	63.54	2.63	VI+	9,085	443	143	4.14
83186	18.9	54.66	3.34	VI+	9,421	498	172	6.11
83187	17.0	43.26	1.63	V+	5,175	417	163	3.77
83188	18.0	45.58	2.86	V+	9,864	548	216	6.27
83190	17.7	41.26	1.45	V+	5,603	210	90	3.51
83194	17.8	46.07	1.56	IV+	4,952	278	107	3.39
83197	17.2	42.14	1.91	V+	6,069	253	144	4.53
83198	16.5	33.86	0.92	IV+	2,921	177	86	2.72
83202	16.0	31.00	0.96	IV+	3,048	190	98	3.10
83204	15.2	28.88	0.94	IV+	2,984	196	103	3.25

Appendix 3. Table 2. Data for female yellow perch collected from Mayatan Lake, Alberta, on 5 December 1984.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
83029	21.0	48.85	7.56	VI+	12,360	588	146	15.48
83210	18.5	53.46	5.85	V+	9,570	517	179	10.94
83211	18.0	50.28	3.44	V+	5,233	291	104	6.84
83212	16.1	37.26	2.25	V+	3,950	245	106	6.04
83213	17.1	49.84	2.12	V+	3,833	224	77	4.25
83214	16.2	35.94	2.37	IV+	4,250	262	118	6.59
83215	16.1	35.71	2.71	IV+	4,716	292	132	7.59
83216	17.8	54.04	3.86	VI+	6,843	384	127	7.14
83217	16.9	41.36	2.92	V+	5,286	313	128	7.06
83218	18.2	53.29	3.51	VI+	5,851	321	110	6.59
83219	16.0	38.76	2.40	V+	4,023	251	104	6.19
83220	15.5	35.28	1.93	IV+	3,516	226	100	5.47
83221	16.9	36.36	2.33	V+	3,883	230	107	6.41
83222	16.3	37.76	2.61	V+	4,750	291	126	6.91
83223	18.6	57.04	2.96	VII+	4,933	265	86	5.19
83224	16.5	36.90	1.26	IV+	2,102	127	57	3.41
83225	17.0	41.74	2.62	V+	4,376	257	105	6.28
83226	18.6	44.37	3.09	VI+	5,150	277	116	6.96
83227	18.5	55.21	4.62	VI+	7,737	418	140	8.37
83228	17.0	43.50	2.50	V+	4,177	246	96	5.75
83229	18.2	49.11	3.54	VI+	6,200	341	126	7.21
83230	18.0	48.37	4.19	V+	7,308	406	151	8.66
83231	16.2	39.53	2.48	IV+	4,133	255	104	6.27
83232	17.4	39.33	2.80	VI+	4,676	269	119	7.12

Appendix 3. Table 3. Data for female yellow perch collected from Mayatan Lake, Alberta, on 14 & 28 January 1984.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
84001	21.2	79.10	9.96	VI+	11,057	522	140	12.59
84002	23.0	102.87	11.88	VII+	13,188	573	128	11.55
84003	18.0	46.78	6.49	V+	7,083	394	151	13.87
84006	20.9	69.98	6.51	VII+	7,227	346	103	9.30
84007	21.2	72.24	3.51	VI+	9,000	427	125	4.86
84010	20.5	64.84	6.61	VI+	8,987	438	139	10.19
84011	16.2	37.67	2.94	IV+	3,141	194	83	7.80
84012	18.2	41.51	4.82	V+	5,568	306	134	11.61
84013	18.0	44.61	3.71	IV+	4,119	229	92	8.32
84014	17.8	47.13	4.37	V+	4,851	272	103	9.27
84015	19.0	44.38	5.62	VI+	6,228	328	140	12.66
84016	18.0	44.49	4.43	VI+	4,742	263	107	9.96
84017	15.5	29.53	3.41	III+	3,785	244	128	11.55
84018	17.0	34.11	2.14	V+	4,069	239	119	6.27
84021	19.0	51.94	5.35	VI+	6,186	326	119	10.30
84022	16.7	33.32	2.18	V+	2,420	145	73	6.54
84030	23.5	108.55	8.11	VI+	9,003	383	83	7.47
84031	14.8	28.82	2.74	III+	2,684	181	93	9.51
84032	23.0	98.90	11.92	V+	13,233	575	134	12.05
84033	20.7	74.94	11.21	V+	12,444	601	166	14.96
84034	18.5	53.89	4.61	V+	4,597	248	85	8.55
84035	19.2	62.34	4.92	V+	6,733	351	108	7.89
84036	19.2	64.62	7.82	V+	6,500	338	101	12.10
84037	20.5	64.52	7.11	V+	8,788	429	136	11.02

Appendix 3. Table 3 ... continuation

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes		GSI
						per cm	per gm	
84038	19.0	53.21	7.23	V+	8,026	422	151	13.59
84039	18.5	52.76	7.14	V+	7,926	428	150	13.53
84040	18.4	48.04	5.41	V+	6,011	327	125	11.26
84041	17.5	38.37	3.59	IV+	3,886	222	101	9.36
84042	17.5	45.13	4.59	V+	4,839	276	107	10.17
84043	17.6	44.59	4.82	IV+	5,351	304	120	10.81
84044	16.8	36.45	3.87	IV+	4,085	243	112	10.62
84085	16.8	39.84	2.88	IV+	3,197	190	80	7.21
84046	17.2	44.93	5.93	IV+	6,583	383	146	13.20
84047	14.2	26.40	1.72	IV+	1,909	134	72	6.52

Appendix 3. Table 4. Data for female yellow perch collected from Mayatan Lake, Alberta, on 27 February 1984.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
84049	18.2	52.64	7.03	V+.	5,400	297	103	13.35
84051	17.5	44.80	7.12	IV+	5,477	313	122	15.89
84052	19.5	63.54	8.12	VI+	6,246	320	98	12.78
84054	15.7	30.89	4.39	III+	3,392	405	140	14.21
84055	20.2	58.26	6.10	VI+	8,172	306	106	10.47
84056	18.9	53.32	8.62	V+	6,538	346	123	16.17
84057	18.6	64.81	9.06	V+	6,923	372	107	13.98
84058	18.1	45.75	5.74	V+	4,385	242	96	12.55
84059	17.1	40.17	4.89	IV+	3,785	221	94	12.17
84062	15.2	31.08	3.54	IV+	4,215	277	136	11.39
84063	16.6	35.65	5.10	IV+	3,923	236	110	14.31
84065	16.4	36.32	5.16	III+	3,979	243	110	14.21
84066	18.0	47.57	6.05	IV+	4,654	259	98	12.72
84067	15.5	27.75	3.38	IV+	2,692	174	97	12.18
84068	21.0	59.42	6.28	V+	7,610	362	128	10.57
84069	16.7	38.61	4.61	IV+	3,546	212	92	11.94
84070	17.0	42.24	6.12	IV+	4,708	277	111	14.49
84072	17.0	41.38	5.03	IV+	3,869	228	93	12.16
84073	17.5	45.05	5.44	IV+	4,269	244	95	12.08
84074	17.7	42.50	6.08	IV+	4,677	264	110	14.31
84078	17.3	42.68	6.03	V+	4,638	268	109	14.13
84080	18.5	47.75	7.71	V+	5,931	321	124	16.15
84084	18.1	58.04	10.58	V+	8,138	450	180	18.23
84085	18.9	52.92	7.85	V+	5,961	315	113	14.83

Appendix 3. Table 4 ... continuation

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
84086	18.5	47.75	8.59	V+	6,610	357	138	17.99
84087	18.5	53.07	7.59	V+	5,877	318	111	14.30
84088	19.5	56.81	9.50	VI+	7,538	387	133	16.72
84089	17.5	39.52	5.04	IV+	3,092	177	78	12.75
84090	16.1	35.90	4.32	IV+	3,292	204	92	12.03
84091	17.1	38.76	4.01	IV+	3,084	180	80	10.35
84092	17.7	40.09	4.81	IV+	3,754	212	94	12.00
84093	15.0	23.49	2.53	IV+	2,411	161	103	10.77

Appendix 3. Table 5. Data for female yellow perch collected from Mayatan Lake, Alberta, on 15 March 1984.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
83097	18.0	46.39	8.50	V+	6,228	346	134	18.32
83098	14.3	24.91	2.80	IV+	2,115	148	85	11.24
84099	19.0	56.34	6.00	V+	9,623	506	171	10.65
84100	18.4	50.17	8.99	V+	6,785	369	135	17.92
84101	17.6	49.26	8.04	V+	8,480	482	172	16.32
84102	18.5	52.77	5.67	V+	4,208	227	80	10.74
84103	19.0	46.24	5.73	VI+	4,454	234	96	12.39
84104	17.5	45.73	4.18	V+	3,169	181	69	9.14
84105	16.2	34.73	4.76	IV+	3,577	221	103	13.71
84106	18.0	42.03	4.23	IV+	3,300	183	79	10.06
84107	17.9	42.79	6.97	V+	5,369	300	125	10.29
84109	15.0	25.26	3.05	III+	2,346	156	93	12.07
84116	18.1	43.16	5.10	V+	3,984	220	92	11.82
84117	16.2	35.54	4.41	IV+	3,577	221	101	12.41
84118	19.7	54.13	10.75	V+	9,023	458	167	19.86
84119	17.6	42.19	6.33	IV+	4,808	273	114	15.00
84120	15.7	30.25	3.59	IV+	2,762	176	91	11.87
84121	17.4	41.74	4.25	III+	3,269	188	78	10.18
84122	18.0	45.10	6.77	IV+	5,146	286	114	15.01
84123	16.5	37.23	3.60	IV+	3,780	229	102	9.67
84124	21.3	76.92	10.08	VII+	7,769	365	101	13.10
84125	21.3	92.61	9.84	VI+	8,577	403	93	10.63
84126	19.0	61.98	8.96	V+	7,292	384	118	14.46

Appendix 3. Table 6. Data for female yellow perch collected from Lac Ste. Anne, Alberta, on 23 February 1983.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
83038	18.5	60.08	9.68	VI+	9,474	512	158	16.11
83039	18.2	57.83	8.04	VI+	8,792	483	152	13.90
83040	18.8	62.58	10.41	VI+	10,622	565	170	16.63
83041	19.2	73.00	14.14	VI+	14,283	744	196	19.37
83044	18.0	59.35	10.20	VI+	10,848	603	183	17.19
83045	18.0	59.91	9.79	V+	9,694	539	162	16.34
83046	17.5	51.39	8.93	V+	9,020	515	176	17.38
83047	18.6	61.28	10.81	V+	10,920	587	178	17.64
83048	18.0	53.03	8.32	VI+	8,928	496	168	15.69
83049	18.0	59.25	8.48	VI+	8,226	457	139	14.31
83050	18.6	70.35	9.77	VI+	9,869	531	140	13.89
83051	18.2	60.75	10.75	VI+	10,859	597	179	17.70
83052	17.5	51.84	5.97	V+	6,030	345	116	11.52
83054	13.6	21.37	3.77	III+	4,315	317	202	17.64
83055	14.2	26.95	4.37	IV+	4,714	332	175	16.22
83057	18.5	61.32	9.04	VI+	9,414	509	153	14.74
83058	16.2	42.21	5.70	V+	5,857	361	139	13.50
83060	15.5	32.31	5.35	IV+	5,404	349	167	16.56
83061	17.5	50.19	8.94	V+	7,898	451	157	17.81
83063	15.5	34.67	5.51	IV+	5,566	359	160	15.89
83064	14.5	30.01	4.86	IV+	5,218	360	174	16.19
83065	15.1	32.83	4.81	IV+	5,242	347	160	14.65
83066	16.5	41.21	5.74	V+	5,998	363	146	13.93
83067	14.2	26.03	3.36	IV+	3,995	281	153	12.91

Appendix 3. Table 6 ... continuation

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
83068	16.2	35.09	4.74	V+	5,836	360	166	13.51
83069	16.2	37.72	4.91	V+	4,660	288	123	13.02
83072	16.1	35.47	5.32	V+	6,764	420	191	15.00
83073	20.0	71.61	11.61	VII+	11,175	559	156	16.21
83074	18.1	53.83	10.40	VI+	9,866	545	183	19.32
83075	18.2	60.44	11.75	VI+	11,869	652	196	19.44
83076	17.6	63.71	9.57	V+	9,866	561	155	15.02
83077	19.5	76.93	11.96	VI+	12,081	619	157	15.55
83079	17.4	52.03	7.87	V+	8,858	509	170	15.13
83080	19.0	61.88	10.57	VI+	10,677	562	172	17.08
83081	19.2	66.66	10.41	V+	10,515	548	158	15.02
83082	15.3	31.03	5.18	IV+	4,461	292	144	16.69
83084	14.6	27.27	3.69	III+	3,333	228	122	13.53
83085	16.8	42.23	7.03	V+	6,399	381	151	16.65
83086	14.3	27.18	4.56	IV+	4,082	285	150	16.78
83087	18.0	59.53	10.82	V+	10,929	607	184	18.18
83089	18.2	54.29	8.60	V+	8,620	474	159	15.84
83090	16.0	34.03	6.01	V+	5,926	370	174	17.66
83091	17.6	51.19	7.96	V+	7,900	449	154	15.55
83092	22.6	116.62	18.63	VII+	19,000	841	163	15.97
83093	18.9	70.66	12.02	V+	12,141	642	172	17.01
83094	15.2	29.30	4.71	V+	4,758	313	162	16.08
83096	17.7	62.[illegible]	11.05	V+	10,988	621	177	17.82
83097	17.2	50.64	8.49	V+	9,014	524	178	16.77
83098	19.6	74.41	11.00	V+	11,100	566	149	14.78
83098	15.0	30.40	5.23	V+	4,981	332	164	17.20
83102	18.0	56.97	10.65	V+	10,757	598	189	18.69

Appendix 3. Table 6 ... continuation

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
83103	19.4	78.25	12.11	VI+	12,233	631	156	15.48
83104	16.6	40.22	6.64	V+	6,902	416	172	16.51
83105	17.8	59.74	7.32	VI+	7,593	427	127	12.25

Appendix 3. Table 7. Data for female yellow perch collected from Lac Ste. Anne, Alberta, on 17 February 1984.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
84002	18.0	63.44	10.61	VI+	11,168	620	176	16.72
84003	19.0	81.44	14.11	VI+	14,532	765	178	17.33
84004	19.5	89.31	17.55	VI+	15,042	771	168	19.65
84005	18.0	62.48	8.96	V+	8,523	474	136	14.34
84006	16.0	43.46	6.98	V+	7,347	459	169	16.06
84007	17.2	54.79	9.77	V+	8,284	482	151	17.83
84008	16.5	42.41	6.76	IV+	7,117	431	168	15.94
84009	15.2	38.06	5.87	IV+	6,178	406	162	15.42
84010	14.5	28.82	5.23	IV+	5,502	379	191	18.15
84011	14.5	30.12	2.89	III+	5,109	352	170	9.59
84012	16.5	45.16	5.90	V+	5,219	316	116	13.00
84013	16.2	42.91	5.93	V+	5,332	329	124	13.82
84014	15.0	41.83	4.16	V+	5,432	362	130	12.34
84015	16.1	45.10	6.57	V+	6,718	417	149	14.57
84016	15.0	34.82	7.77	IV+	5,812	387	167	22.31
84017	15.2	36.34	5.31	IV+	5,898	388	162	14.61
84019	15.6	36.48	5.60	IV+	5,964	382	163	15.35
84020	14.5	27.50	3.97	III+	5,117	353	186	14.44
84021	12.8	19.98	2.38	III+	2,505	196	125	11.99
84022	16.4	46.60	8.13	V+	5,359	327	115	17.45
84023	16.2	42.51	6.51	V+	6,861	423	161	15.31
84024	15.5	38.83	6.06	IV+	5,017	324	129	15.61
84025	14.5	28.13	4.88	IV+	5,170	357	184	17.35
84026	13.0	25.54	3.28	III+	3,452	265	135	12.84

Appendix 3. Table 7 ... continuation

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
84028	14.0	25.68	2.96	IV+	4;064	290	158	11.53
84029	12.6	20.48	2.37	III+	2,487	197	121	11.57
84030	18.2	61.89	10.73	V+	9,710	533	157	17.34
84031	17.8	57.23	8.58	V+	7,590	426	133	14.99
84032	16.7	39.35	6.20	V+	6,804	407	173	15.76
84033	17.0	45.70	8.11	V+	7,511	442	164	17.75
84034	15.9	34.57	5.30	IV+	5,860	369	170	15.33
84035	13.1	19.98	2.89	III+	2,984	228	149	14.46
84036	14.0	22.23	3.24	III+	3,411	244	153	14.57
84037	14.0	24.27	3.90	III+	4,105	293	169	16.07
84038	13.0	21.96	3.96	III+	4,170	321	190	18.03
84040	12.5	16.59	2.30	III+	2,421	194	146	13.86

Appendix 3. Table 8. Data for female yellow perch collected from Thunder Lake, Alberta, on 22 February 1984.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
84001	22.0	96.09	16.28	VI+	18,292	831	190	16.94
84002	20.5	81.09	12.01	V+	12,492	609	154	14.81
84005	20.5	83.35	13.76	V+	15,460	754	185	16.51
84006	19.0	66.11	8.51	IV+	9,570	504	145	12.87
84007	19.3	64.63	10.11	IV+	10,735	556	166	15.64
84008	20.5	75.34	11.94	IV+	13,416	654	178	15.85
84009	20.0	71.37	8.84	IV+	9,932	497	139	12.39
84010	20.1	76.11	9.44	V+	10,700	532	141	12.40
84012	19.4	65.17	10.54	V+	11,842	610	182	16.17
84013	18.5	64.48	10.07	IV+	11,301	611	175	15.62
84014	19.5	69.24	9.52	IV+	10,685	548	154	13.75
84015	18.2	55.37	6.98	IV+	7,852	431	142	12.61
84016	20.8	77.90	10.09	IV+	11,377	547	146	12.95
84017	19.2	62.59	9.01	IV+	10,123	527	162	14.40
84018	18.5	59.76	10.46	IV+	11,752	635	197	17.50
84020	17.0	47.97	6.46	V+	5,258	309	110	13.47
84021	18.0	63.76	8.27	IV+	10,292	572	161	12.97
84022	19.0	57.58	7.07	IV+	7,943	418	119	12.28
84024	19.0	56.99	7.86	IV+	8,832	465	155	13.79
84025	16.5	40.04	5.16	IV+	4,997	303	125	12.89
84026	18.0	50.38	7.19	V+	8,090	449	161	14.27
84027	19.0	68.00	7.21	IV+	8,101	426	119	10.60
84029	18.1	56.04	9.31	IV+	9,461	523	169	16.61
84030	17.0	50.77	6.73	III+	7,562	445	149	13.26

Appendix 3. Table 8 ... continuation

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes per cm	Developing oocytes per gm	GSI
84031	17.0	44.43	4.61	IV+	5,079	299	114	10.38
84032	18.4	49.76	6.49	III+	7,292	396	146	13.04
84033	20.0	70.85	10.83	IV+	12,200	610	172	15.29
84034	17.0	50.95	7.16	III+	8,045	457	158	14.05
84036	17.8	49.06	6.68	IV+	7,505	422	153	13.62
84037	17.5	47.02	6.43	IV+	7,225	413	154	13.68

Appendix 3. Table 9. Data for female yellow perch collected from Narrow Lake, Alberta, on 23 February 1984.

Sample Number	Total Length (cm)	Somatic Weight (gm)	Ovary Weight (gm)	Age (years)	Fecundity	Developing oocytes		GSI
						per cm	per gm	
84001	16.5	35.68	7.60	VI+	8,935	542	250	21.30
84002	14.2	24.76	5.63	V+	6,481	456	262	22.74
84003	12.0	14.79	2.79	IV+	3,295	275	223	18.80
84004	13.9	22.34	6.49	V+	7,460	537	334	39.05
84005	14.2	23.36	4.84	V+	5,560	392	238	20.72
84006	16.1	33.90	7.94	V+	10,124	629	299	23.42
84008	11.5	13.27	2.33	III+	2,678	233	202	17.56
84009	11.0	11.76	1.98	III+	2,276	207	194	16.84
84010	9.9	8.25	1.52	II+	1,747	212	176	18.42